

## Sunfish foraging among patches: the patch-departure decision

DENNIS R. DEVRIES, ROY A. STEIN & PETER L. CHESSON  
*Department of Zoology, The Ohio State University, Columbus, OH 43210, U.S.A.*

**Abstract.** Patch-use behaviour of small bluegill sunfish, *Lepomis macrochirus*, foraging for chironomid larvae, *Chironomus riparius*, was investigated in artificial macrophyte patches to examine search pattern within a patch and to determine the decision rule used by fish when leaving a patch. Fish were exposed to a sequence of habitats which differed in quality (i.e. total prey density); however, within a habitat all patches were of equal quality. When foraging in a single patch, fish encountered prey randomly, as evidenced by agreement between the distribution of intercapture intervals and the exponential distribution. Agreement between fish behaviour and predictions of a rate decision rule indicated that the decision to leave a patch was based on some estimate of capture rate in the patch. Predictions of how long fish should stay in a patch and how many prey they should capture during a patch visit were generated, using a giving-up time model based on an exponential distribution of intercapture intervals. Fish generally stayed longer and captured more prey than predicted by the model, using giving-up times that were longer than optimal. The relationship between rate of prey capture for the habitat and giving-up times was shaped such that fish minimized the cost, in terms of a decrease in capture rate, by overestimating rather than underestimating the optimal giving-up time.

Under the assumptions of optimal foraging theory animals that forage for patchily distributed prey in the absence of predators decide how to exploit patches so as to maximize their net energy intake rate (Pyke et al. 1977; Pyke 1984). We examine how foragers search within a patch and then concentrate on how long they should remain in a patch. We first determine how the decision to leave a patch is made and then use this information to predict how long foragers should remain in the patch. Throughout this paper, we use the term habitat as the heterogeneous environment in which an organism is foraging, whereas the term patch represents a homogeneous subset of the habitat.

To exploit patches, the best strategy a forager can use depends on both the distribution of prey among patches and the amount of information used in making decisions. A forager that searches randomly for prey, which become depleted within a patch, experiences decreased capture rate over time in the patch (Charnov et al. 1976). Because of this decrease, foragers must decide at what point of prey depletion to move to another patch (Charnov 1976). This decision has received much attention in the optimal foraging literature (see summary in Krebs et al. 1983). Calculation of the best time to leave a patch can be complex (e.g. Oaten 1977) and foragers are generally thought to use simple behavioural decision rules to approximate the optimal

solution (Breck 1978; Cowie & Krebs 1979; Iwasa et al. 1981; Janetos & Cole 1981).

Three types of decision rules have been considered most often: (1) a time decision rule, where the forager remains in a patch for some particular amount of time; (2) a number decision rule, where the forager remains in a patch until it captures some particular number of prey; and (3) a rate decision rule, where the forager remains in a patch until capture rate in that patch decreases to some threshold level (Krebs et al. 1974; Charnov 1976). The particular amount of time, number of prey, or threshold capture rate that is used by the forager must be based on foraging experience in the system, and the best decision rule to use depends on the distribution of prey among patches (Iwasa et al. 1981).

To determine how foragers decide when to leave a patch, several approaches have been used, often varying habitat or patch quality. To determine how great tits, *Parus major*, decide to leave a patch, Cowie (1979) altered habitat quality and observed changes in time spent in a patch (see also Zach & Falls 1976). However, more often both patch quality and habitat quality are varied (e.g. Krebs et al. 1974; Lima 1983, 1984). In contrast, Marschall et al. (1989) varied patch quality within habitats, keeping habitat quality constant across treatments in their study of patch-use behaviour of small

bluegills, *Lepomis macrochirus*. Here we also present a study of patch-use behaviour of small bluegills; however, we altered habitat quality (i.e. total prey density differed across habitats or treatments) and kept patch quality constant within a habitat (i.e. prey density is the same across patches within a habitat or treatment).

In this paper we quantify behaviour of small bluegill foraging in simulated macrophyte patches in laboratory pools. Patch-use behaviour of small bluegill is important because they are often constrained to vegetated littoral areas of lakes due to risk of predation from largemouth bass, *Micropterus salmoides* (Werner et al. 1983). In these areas, prey resources may be limiting and competition (both interspecific and intraspecific) can be intense (Mittelbach 1984; Mittelbach & Chesson 1987). Because prey are often distributed in patches, a premium will be placed on efficiently exploiting these patches of prey. Within this context, we are specifically concerned with the following questions. (1) What is the within-patch search strategy of small bluegill? (2) How do these bluegill decide when to leave a patch? (3) Given the within-patch search strategy and decision rule of small bluegill, can we predict their patch residence times?

## METHODS

### Experimental Design

Small bluegill (45–80 mm total length) were trained to forage in simulated macrophyte patches. Patches (36 × 42 cm) consisted of a Plexiglas base with green rope (3 mm diameter) attached to the base such that the free ends floated to the water surface, simulating natural macrophyte stems. Stem density in patches was 1000 stems/m<sup>2</sup>. Prey in all experiments were 10–12-mm midge larvae, *Chironomus riparius*, that were frozen, thawed, and attached to the stems with a small amount of aquarium sealant, simulating clinging prey. Fish were held at 25°C between experiments and were satiated with dry food 24 h before an experiment. Experiments were run at 25°C.

Experiments were run in a circular pool (1.75 m diameter, 0.3 m deep) that was divided into four compartments, each containing one patch. Partitions between patch compartments contained doors that closed when fish left the patch compartments, preventing revisits. Within an experiment all patches that fish entered had the same prey

density. As the fish foraged, we recorded when fish entered and left a patch, when prey were captured, obvious time spent handling prey, and time spent motionless in a patch. Handling times that were too short to be observed were measured from filmed experiments. An experiment began when one bluegill was released into the first patch compartment and ended after it had travelled through all four patches and left the fourth patch or when it remained motionless in a patch for more than 2 min. Fish generally did not appear to realize that only four patches were present in the pool habitat and they left the fourth patch toward the closed door before the first patch just as they had left the previous three patches. To be considered a complete patch visit the fish had to enter the patch and subsequently leave the patch with a burst of speed toward the door to the next patch. When an experiment ended because the fish stopped foraging in a patch, results from that patch visit were not included in any data analyses. This occurred in only 7.5% of all patch visits and was due to satiation, most often at high prey density. Fish that stopped foraging in a patch showed no indications of satiation (which was easily distinguished from normal foraging behaviour) before the patch visit during which they stopped. By excluding these incomplete patch visits, all data should represent similar hunger levels. In addition, fish sometimes left a patch with a burst of speed toward the next patch, but did not find the door to the next patch as they approached the partition, causing them to re-enter the previous patch. Because it appeared that fish simply did not find the door rather than deciding to return to the previous patch, we did not include the extra patch visit time in residence time in the patch. When fish found the door to the next patch on a later approach to the partition, we included subsequent patch-use data in our analysis.

All fish were run through the same sequence of treatments (Table I). Before any data were collected, fish were trained to forage in the four-patch system. Training ended when fish foraged in and left all four patches. After training, we recorded data for each bluegill during five to eight experiments in the low prey density treatment (six prey/patch) and then nine experiments at 12 prey/patch. During the first high density experiments fish may have still expected the low prey density treatment or may have had an uncertain expectation of prey density. Therefore, the first three of these experiments were arbitrarily considered a transition

**Table I.** Sequence of experimental treatments through which all bluegills were run

Treatment	Number of experiments	Prey density (prey/patch)
Training (pool)	5-15	6
Low prey density (pool)	5-8	6
Transition (pool)	3	12
High prey density (pool)	6	12
Transition (pool)	3	6
Filmed acclimation with quartz lights (pool)	2	6
Filmed experiment (pool)	1	6
Low prey density (one-patch)	4	6
Filmed experiment (one-patch)	1	6

treatment. Following these transition experiments, fish were likely to have begun to expect a high prey density so the next experiments were grouped as the high prey density treatment. After these, fish were returned to low prey density (again, a three-experiment transition treatment), acclimated to foraging while quartz photographic lights were shone on the pool, and filmed. After pool experiments, behavioural data were collected for each bluegill in five experiments in which the fish was constrained to a single patch (which we refer to as one-patch experiments). The fifth one-patch experiment was filmed. To film experiments we used 16-mm movie equipment at a film speed of 24 frames/s.

#### Within-patch Search Strategy

Data from the first four one-patch experiments were used to test whether search by bluegill within a patch was random and whether capture rate within a patch decreased as they foraged. The model of random searching that we used was described previously by Marschall et al. (1989). Here, we review briefly the details of this model, which was based on two assumptions: (1) individual prey were encountered and captured independently of other individual prey, and (2) the conditional probability of capturing an individual prey during the next interval of time, given that it had not been captured already, depended only on the length of that interval and not on previous unsuccessful search time. These assumptions lead to an exponential distribution of capture times. If capture times are exponentially distributed, then the time to capture

the first prey when  $N$  prey are present (i.e. the intercapture interval, preceding the  $n^{\text{th}}$  prey) is also exponentially distributed. So if bluegills are searching randomly within patches, the distribution of intercapture intervals,  $T_n$ , at a given prey density,  $n$ , should not differ from the exponential distribution, and should have a mean inversely proportional to  $n$ . To test this we used the following two tests (Marschall et al. 1989). The first test uses the statistic  $W_n^2$  (Pearson & Stephens 1962; Seshadri et al. 1969) and tests the hypothesis that the shape of the distribution is exponential, assuming that the mean is inversely proportional to  $n$ . The second test is a chi-squared test of the hypothesis that the mean is inversely proportional to  $n$ , assuming that the distribution is exponential.

To examine search path within a patch, we calculated a turning index for each patch visit of each bluegill from filmed pool experiments. This turning index was defined as follows

$$\text{turning index} = \frac{\text{actual distance travelled in a patch}}{\text{maximum linear dimension of the searched area}} \quad (1)$$

Turning index values describe the non-linearity of a search path within a patch. The minimum value of this index is 1, which occurs when the fish moves in a straight line through a patch; it increases as the fish turns more during search and increases its search effort in a patch. Although similar to the meander ratio (Williamson & Gray 1975), the turning index has a less variable denominator (i.e. it cannot decrease to 0 as that of the meander ratio can) and is thus likely to have better statistical properties.

#### Patch-departure Decision

The increase in habitat quality in the sequence of low, transition, and high prey density treatments (Table I) was designed to aid in distinguishing among three types of simple behavioural decision rules that bluegills might use to decide when to leave patches. We considered three decision rules that are both the simplest that a forager can use and are the rules found most commonly in the literature: (1) a time decision rule, (2) a number decision rule, and (3) a rate decision rule. When habitat quality is increased, predictions of these three decision rules differ in terms of three types of data (Cowie & Krebs 1979; Hodges 1981): (1) residence time in a patch during a patch visit, (2) number of prey captured in a patch during a patch visit, and

(3) giving-up time for a patch during a patch visit (where giving-up time is the time between the last prey capture in a patch and the time that the forager leaves the patch; Krebs et al. 1974). A fish using a time decision rule should stay the same amount of time, eat more prey, and have a shorter giving-up time when moved from six prey/patch to 12 prey/patch. Using a number decision rule, a forager should stay a shorter amount of time and eat the same number of prey when moved from six prey/patch to 12 prey/patch. When prey density is increased, the expected change in giving-up time by a forager using a number decision rule is unclear. If fish leave immediately after the last prey capture, then giving-up time will not change when prey density is increased; but if, after the last prey capture, fish have to travel through the patch as they exit, then the change in giving-up time cannot be predicted. A fish using a rate decision rule should stay longer, eat more prey, and have the same giving-up time when moved from six prey/patch to 12 prey/patch.

These predictions are made under the assumption that fish have not learned that the environment with 12 prey/patch differs from the environment with six prey/patch. If bluegills do learn and are attempting to be efficient in their foraging, then significant differences should be found between the data from transition and high prey density treatments. The change in behaviour will occur as bluegills adjust their patch-departure rule to account for the new conditions. Thus, by increasing prey density, we could determine the type of decision rule that bluegills used to leave patches and examine whether they adjusted their behaviour with experience at the increased prey density.

## RESULTS

### Within-patch Search Strategy

Seven fish (different individuals from those used by Marschall et al. 1989) were trained to forage in this four-patch system. An analysis of variance revealed that recovery times (i.e. the short portion of handling time that had to be measured from filmed experiments) did not differ among individuals so we averaged across individuals and estimated it to be 0.025 min (SD = 0.006 min,  $N = 62$  total observations). We subtracted this value from residence time in a patch for all prey captures for all fish. For all fish the distribution of  $T_r$  did not differ

**Table II.** Turning index values for each patch visit for each bluegill in filmed experiments

Fish	Patch				Mean (SD)
	1	2	3	4	
1	1.60	1.12	1.18	1.18	1.27 (0.22)
2	1.01	1.62	1.08	1.32	1.26 (0.28)
3	1.71	1.14	1.17	1.26	1.32 (0.27)
4	4.29	1.43	1.11	—	2.28 (1.75)
6	3.32	3.21	1.26	1.09	2.22 (1.21)
7	3.17	1.22	3.21	2.97	2.64 (0.96)

from the exponential distribution ( $P > 0.20$ ). In addition, we could not reject the hypothesis that the mean was inversely proportional to  $n$ , given that the distribution was exponential (chi-squared test,  $P > 0.50$ ). Thus, the data were consistent with the hypothesis that intercapture intervals were exponentially distributed and bluegills searched randomly within patches.

An examination of turning indices measured from filmed experiments indicated that while searching within a patch, bluegills appeared to use two different strategies (Table II). Some fish (fish 1, 2 and 3) travelled straight through patches with little turning, and for these individuals turning indices were relatively small for all four patches. In contrast, fish 4, 6 and 7 turned more frequently and, over all four patches, these fish had higher turning indices than the first group. We compared turning indices of the two groups of fish with an a posteriori  $t$ -test (two-sample, two-tailed) and found they differed ( $P = 0.004$ ), supporting the idea that the two groups of fish used different search paths.

### Patch-departure Decision

To determine how bluegill decide to leave a patch, changes in residence time, number of prey eaten, and giving-up time in a patch were compared among low, transition and high prey density treatments with a two-way analysis of variance. Residence time, number of prey eaten, and giving-up time in a patch were averaged across patches within an experiment, and experiments within a treatment

**Table III.** Mean values and results from the two-way ANOVA for residence time, number of prey captured, and giving-up time for patch visits to 6-prey patches (low prey density treatment) and 12-prey patches (transition and high prey density treatments)

	Type of data					
	Residence time		Number captured		Giving-up time	
	6-prey	12-prey	6-prey	12-prey	6-prey	12-prey
Fish 1	0.231	0.218	2.83	4.59	0.047	0.054
Fish 2	0.181	0.169	2.21	4.80	0.072	0.057
Fish 3	0.210	0.392	2.45	7.78	0.103	0.114
Fish 4	0.217	0.393	3.38	7.49	0.064	0.091
Fish 5	0.108	0.282	2.34	5.61	0.033	0.052
Fish 6	0.187	0.351	3.20	7.38	0.062	0.042
Fish 7	0.161	0.314	3.10	7.19	0.064	0.054
<i>ANOVA results</i>						
Prey density	$P < 0.001$		$P < 0.001$		$P = 0.93$	
Fish	$P < 0.01$		$P < 0.001$		$P = 0.01$	
Prey density $\times$ fish	$P = 0.17$		$P = 0.37$		$P = 0.21$	

were considered replicates. Log transformations of residence time, number of prey captured, and giving-up time were used to normalize the data. Multiple comparisons indicated that all significant differences ( $P < 0.05$ ) among treatments were between either low and transition prey density treatments or low and high prey density treatments. No comparisons of transition and high prey density treatments differed. Thus, fish did not appear to modify their foraging behaviour as they gained experience at 12 prey/patch. Changes in residence time, number of prey eaten, and giving-up time occurred immediately when the fish began foraging at a prey density of 12 prey/patch. When compared among treatments, residence time and number of prey eaten in a patch were both significantly affected by prey density treatments and fish identity, but in both cases interaction terms were not significant (Table III). Residence time and number of prey eaten in a patch increased significantly as prey density was increased (Table III). Giving-up time differed for different fish but was not affected by prey density or the interaction term (Table III). Non-significant interaction terms for residence time and number of prey eaten in a patch indicate that, in general, fish spent more time searching in a patch and capturing more prey as prey density increased. The increase in residence time and number of prey eaten in a patch, and no change in giving-up time as prey density increased, agrees with the predictions of a rate decision rule.

Given this qualitative agreement between bluegill behaviour and predictions of a rate decision rule, we will now use this decision rule to generate quantitative predictions for comparison with bluegill behaviour.

#### A Giving-up Time Model

A forager using a rate decision rule to decide when to leave a particular patch bases its decision to leave on information gained while foraging in that patch. This information allows the forager to assess when the giving-up time has been exceeded. Because bluegills used a rule based on capture rate to decide when to leave a patch, a model designed to generate quantitative predictions of optimal patch residence time must incorporate the fact that fish based their decision to leave on information gained while foraging. Iwasa et al. (1981) and McNair (1982) described a model designed to predict optimal residence time in a patch for a forager using a rate (or giving-up time) decision rule (for a similar derivation see Breck 1978). The model is based on the assumption that the forager leaves a patch when the time since the last prey capture exceeds some value, fixed for each patch type, the giving-up time for that patch type. No empirical tests of this model have been conducted, probably because of the difficulty in describing the distribution of intercapture intervals with a probability distribution.

The giving-up time model is based on the assumption that the forager recognizes a patch type before foraging in it and uses the same giving-up time throughout its visit in that patch type (McNair 1982). Although unrealistic in some systems, this assumption is reasonable here because all patch types were identical, containing six prey during both training and the low prey density treatment. Thus, we expected fish to recognize and behave as if all patches were the same during all low prey density experiments. McNair (1982) presented an example in which the mean time to capture the first prey in a patch is shorter than subsequent mean intercapture intervals in that patch, which he assumed are all equal. For our system, however, intercapture intervals are exponential with mean  $1/(an)$ , where  $n$  is the number of prey left in the patch at the beginning of the intercapture interval. Thus, we need to modify McNair's development for our situation.

McNair (1982) stated that the quantity to be maximized is the rate of energy intake for the habitat (i.e. for the entire system of patches). In our system we used capture rate rather than energy intake rate because the energetic value of one prey item is at least one order of magnitude greater than the cost of searching for and handling a prey item.

Because all patches were identical, we defined the quantity to be maximized to be  $\xi_\tau$ , the habitat rate of prey capture associated with a giving-up time of  $\tau$ , where

$$\xi_\tau = \frac{E(Y_m)}{E(R_m) + T} \quad (2)$$

where  $E(Y_m)$  is the expected yield in a patch initially containing  $m$  prey,  $E(R_m)$  is the expected residence time in a patch initially containing  $m$  prey, and  $T$  is the average travel time between patches. The giving-up time, on which both  $E(Y_m)$  and  $E(R_m)$  depend, is chosen such that  $\xi$  is maximized. The expression for the expected number of prey captured in a patch (i.e. the yield,  $E(Y_m)$ ) is

$$E(Y_m) = \sum_{n=1}^m nP_n \quad (3a)$$

$$= \sum_{n=1}^m (ne^{-(m-n)\alpha\tau} \prod_{i=0}^{n-1} (1 - e^{-(m-i)\alpha\tau})) \quad (3b)$$

where  $m$  is the number of prey in the patch at the start of the patch visit,  $P_n$  is the probability of capturing  $n$  prey during a patch visit with a giving-up time of  $\tau$ ,  $\alpha^{-1}$  is the mean of the exponential distribution, and  $\tau$  is the giving-up time. The expected residence time in a patch containing  $m$  prey,  $E(R_m)$ , is

**Table IV.** Predicted and actual residence time and number of prey captured in a patch

Fish	Residence time (min)			Number captured		
	Predicted*	Actual†	$P_\ddagger$	Predicted	Actual	$P$
1	0.12	0.231 (0.240)	0.034	1.58	2.83 (1.81)	0.003
2	0.12	0.181 (0.119)	0.018	1.44	2.21 (1.42)	0.008
3	0.12	0.210 (0.164)	0.028	1.68	2.45 (1.93)	0.091
4	0.10	0.216 (0.121)	0.001	2.12	3.32 (1.53)	0.003
5	0.14	0.108 (0.070)	0.024	1.30	2.34 (1.18)	< 0.001
6	0.11	0.187 (0.089)	0.001	1.50	3.20 (1.32)	< 0.001
7	0.14	0.161 (0.113)	0.482	1.25	3.10 (1.71)	< 0.001

\* Predicted values are from an optimal giving-up time model based on an exponential distribution of intercapture intervals.

† Actual data are means (SD) from patch visits by each fish in pool experiments at low prey density (six prey/patch).

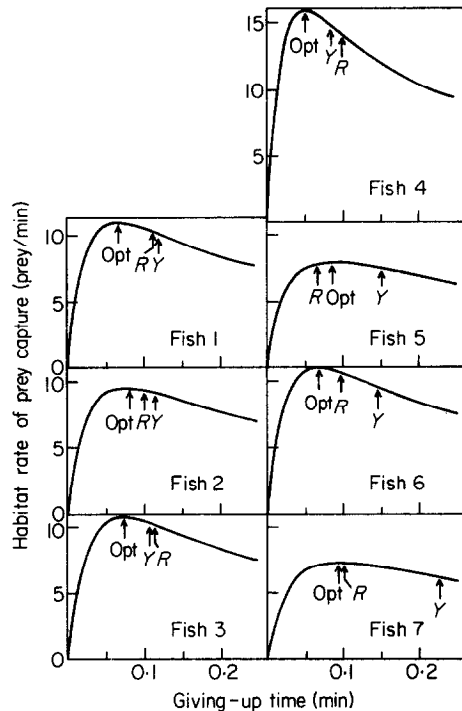
‡ Probability values are from a one-sample, two-tailed  $t$ -test.

$$E(R_m) = \sum_{i=1}^m \left( \frac{1}{i\alpha} \prod_{j=1}^m (1 - e^{-j\alpha\tau}) \right) + \tau \prod_{i=1}^m (1 - e^{-i\alpha\tau}) \quad (4)$$

The quantity  $\alpha^{-1}$  was calculated as the mean of the values of  $nT_n$  from one-patch experiments for each fish (as in Marschall et al. 1989). Travel times were taken as the average travel time between patches from pool experiments for each fish. The resulting equation was solved for the value of  $\tau$  that gave the maximum  $\xi$ , that is, the optimal giving-up time ( $\hat{\tau}$ ). As expected,  $\xi$  rose to a single peak and then declined to 0 as  $\tau$  increased (Fig. 1). Equations (3b) and (4) were solved at  $\tau = \hat{\tau}$  for the number of prey captured ( $E(Y_m)$ ) and residence time ( $E(R_m)$ ), respectively, that were predicted by the model for a forager using the optimal giving-up time as its cue to decide when to leave a patch.

To compare predictions of the optimal giving-up time model with data from our bluegill foraging experiments, we used a one-sample, two-tailed *t*-test to compare  $E(R_m)$  and  $E(Y_m)$  at  $\hat{\tau}$  to the actual mean residence time and number of prey captured for each fish in the low prey density treatment. We chose to compare model predictions and actual behaviour for residence time and number of prey captured rather than predictions and actual behaviour for giving-up times for several reasons. Giving-up times were short relative to the accuracy of the behaviour recorder (giving-up time values, 95% confidence limits over all seven fish = 0.065–0.085 min; behaviour recorder accuracy = 0.01 min) and thus our measurements of giving-up time were more variable and were probably less accurate than our measurements of residence time and number of prey captured. In addition, if fish were at the end of the patch farthest from the door to the next patch, then they had to travel through the length of the patch before exiting. This would alter the average value of giving-up time from that which fish intended to use, again decreasing the accuracy of our estimate of giving-up time.

In general, fish stayed longer and captured more prey than predicted by the optimal giving-up time model (Table IV). In only one comparison (fish 5, residence time) was the actual behaviour less than the predicted behaviour. A graph of  $\xi$  as a function of giving-up time shows that, for all fish,  $\xi$  rises sharply to a peak (the habitat rate of prey capture at the optimal giving-up time), then decreases



**Figure 1.** Graph of the habitat rate of prey capture ( $\xi = E(Y_m)/(E(R_m) + T)$ ) as a function of giving-up time for the seven fish. The point labelled Opt is the giving-up time required to produce the maximum habitat rate of prey capture. The points Y and R represent the giving-up times (and associated capture rates) that were necessary to produce the fish's actual average yield and average residence time, respectively, using the giving-up time model. Actual data are means from patch visits in the low prey density treatment.

gradually with further increase in giving-up time (Fig. 1). To determine the value of giving-up time that was required for the model to output the bluegill's actual mean residence time or mean number of prey captured, we substituted giving-up time values into equations (3b) and (4) until the yield or residence time, respectively, predicted by the model was equal to the actual residence time or yield. These backcalculated giving-up times were greater than the predicted optimal giving-up times in 13 of 14 cases (Fig. 1). In a similar manner, we determined the giving-up time values required for equations (3b) and (4) to produce the actual values of the 95% confidence limits of actual yield and actual residence time, respectively. This produced 95% confidence limits around the backcalculated giving-up times. In 11 of 13 comparisons the lower

95% limit of the backcalculated giving-up time was greater than or equal to the predicted optimal giving-up time. Thus, fish used giving-up times that were longer than the optimal giving-up time.

## DISCUSSION

Because fish used a rule based on capture rate to decide to leave patches, a model to describe the optimal behaviour must take this into account. It is important to recognize that a model of optimal patch use does not necessarily describe the mechanism by which the forager achieves the optimal solution. Foragers are usually assumed to maximize energy intake rate in a patchy system but may use criteria other than capture rate (e.g. residence time in the patch or number of prey captured in the patch) to approximate the optimal solution. It is because of this that the marginal value theorem (Charnov 1976) cannot be used to describe behaviour of a forager that uses a rate decision rule. For a forager that does not use information gained while foraging in a patch to decide when to leave the patch, marginal value theorem is an appropriate model (McNair 1982; Stewart-Oaten 1982). However, a forager that uses information gained during patch visits behaves under a different set of conditions from those experienced by a forager that does not use this information (i.e. it has more information about the patch). These two foragers cannot be expected to follow predictions from the same model. For this reason a model based on a giving-up time decision rule, where the forager is assumed to use information gained during patch visits, is appropriate for a forager using a rate decision rule (McNair 1982).

Predictions of the optimal giving-up time model consistently underestimated residence time and number of prey captured for all fish (i.e. in 13 of 14 comparisons; differences were significant in 11 of 14 comparisons). Several hypotheses may explain this behaviour. Because the slope of  $\xi$  as a function of giving-up time is steeper to the left than to the right of the peak of the curve, fish encounter a greater cost, in terms of a decrease in capture rate, by underestimating, rather than overestimating, the optimal giving-up time. That is, it is less costly for a fish to stay in a patch too long than to leave too early after a prey capture. If fish cannot accurately assess the optimal giving-up time, they would do better to overestimate it than to under-

estimate it. Additionally, the longer giving-up time may allow fish to sample patch quality, although we have no way to test for this at present. Finally, the extra giving-up time may simply be an artefact of the experimental set-up. If fish were at the end of the patch farthest from the next patch when the giving-up time was exceeded, then they travelled the length of the patch before exiting the patch. This would lead to longer residence time and giving-up time than predicted by the model but would probably not lead to increased prey captures, unless fish found additional prey items as they travelled through the patch to exit. This did not appear to be the case during experiments and, because all fish captured more prey than predicted, we suggest that fish were estimating the giving-up time conservatively.

The finding that bluegill used a rate patch-departure rule differs from the results of Marschall et al. (1989). In their experiments, habitat quality was always constant (i.e. total prey density remained constant across habitats), but patch quality (i.e. prey density in a patch) was variable within a habitat. In our system, we exposed fish to habitats which varied in quality (i.e. total prey density varied across habitats), but within a habitat, patches were all of equal quality (i.e. all patches within a habitat had equal prey densities). In addition, their experimental design allowed fish to revisit patches, so not only did capture rate within a patch decrease during a patch visit (due to random searching within a patch) but capture rate for the entire habitat (including all patches) also decreased over the course of an experiment. Without patch revisitation, as in our system, capture rate within a patch decreases, but average capture rate for the system does not change as the bluegill forages. Marschall et al. (1989) found that, in their system, bluegill behaviour is not completely consistent with predictions of any of the three simple decision rules but is most similar to a residence-time decision rule. Given the differences in the system used in this study and that of Marschall et al. (1989), these results suggest that bluegills might be able to assess characteristics of the environment in which they forage (e.g. patch-depletion characteristics) and use a different patch-departure rule based on those characteristics.

In one-patch experiments, fish foraged randomly within patches. This result supports conclusions of Marschall et al. (1989) who also found that juvenile bluegills searched randomly within patches. Based



on turning-index analysis, fish differed in their within-patch search paths. However, they all searched patches randomly, using a rate decision rule to decide when to leave a patch. Thus, differences in search-paths did not carry over into these other patch-use behaviours.

Our data have supported that bluegills search randomly within a patch and we found that individuals use different search-path strategies within a patch. Of the three simple decision rules that we examined, fish behaviour was consistent with predictions of a rate patch-departure rule. We generated quantitative predictions of residence time and number of prey captured in a patch for a forager that used a rule based on capture rate to decide when to leave a patch, and found that fish stayed longer and captured more prey than predicted. The difference between actual and predicted behaviour was in a direction that minimized the cost of poorly approximating the optimal solution.

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