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Swimming response of goldfish, *Carassius auratus*, and the tetra, *Hemigrammus caudovittatus*, larvae to individual food items and patches

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Synopsis

Swimming speed and swimming path of goldfish and tetra larvae were studied in aquaria containing food patches composed of decapsulated cysts and immobilized nauplii of *Artemia salina* or sparsely distributed prey. The mean swimming speed of starved larvae in the medium without food was about four times higher than the speed of larvae feeding in a patch. Satiated larvae swam about 1.5 times slower than hungry fish. Consumption of single prey items by starved larvae caused the following sequence of swimming responses: 'handling pause' (cessation of swimming), slow swimming in a restricted area, and fast swimming (approximately twice as fast as hungry larvae before encountering food) accompanied by a widening of the area searched ('area increased searching'). Mean swimming speed was constant over a broad range (10^1–10^3 ind·l^{-1}) of food density, although at extreme (high or low) values of food density it depended on swimming responses of the predator. Frequency of visits to the different parts of the aquarium strongly depended on encounters of hungry fish with food particles or patches.

Introduction

Swimming speed, swimming path, duration of stops and movement periods are important elements of fish foraging behaviour, especially during early life stages (Braum 1967, Rosenthal & Hempel 1970, Blaxter & Staines 1971, Hunter & Thomas 1974, Munk & Kiorboe 1985). Mean swimming speed and reaction distance are the main components of some mathematical models of food consumption by solitary fish (Rashevsky 1959, Ware 1975, Vlymen 1977, Dabrowski et al. 1988). Swimming speed in these models is assumed constant and does not depend on food abundance and distribution. This assumption is supported by some experimental results (Ivlev 1944, Mikheev & Pakulska 1988). However, there are some data suggesting that swimming speed of fish larvae depends on prey density (Hunter & Thomas 1974, Munk & Kiorboe 1985) – a decrease of prey density leads to an increase of swimming speed. The possible source of the discrepancy is the difference in the prey density range. In the first case, density values varied in the range of 10–1000 ind · l^{-1}; in the second case, 1–100 ind · l^{-1}.

We suppose that at low prey densities a foraging fish controls its prey encounter rate by modifying swimming speed; if prey density is relatively high the encounter rate at a low and constant swimming speed is enough to support the necessary ingestion rate. To understand how a foraging fish behaves and controls its swimming at different levels of food

abundance we have to know its swimming response to individual food particles and/or to aggregations of these particles.

There is some evidence showing changes of swimming path (Beukema 1968, Thomas 1974), run length, run turn angle and pause duration (O'Brien et al. 1986, Evans & O'Brien 1988, O'Brien et al. 1989) just after consumption of prey. In foraging models with mean swimming speed as one of the main components it is necessary to know: first, whether swimming speed and swimming path of a foraging fish depend on its interaction with food particles consumed and, second, whether it is enough to know the results of such interactions to predict the swimming characteristics of a fish foraging in the food patch.

In this paper we present some experimental results on swimming of goldfish and tetra larvae in different foraging situations: hungry fish in an aquarium without food, fish in an aquarium with sparsely distributed food particles, and fish in a dense food patch.

Materials and methods

Experiments were carried out in March–July 1987. Goldfish (GF) and tetras (BT) larvae were raised in the laboratory from eggs, fed with nauplii and decapsulated cysts of *Artemia salina,* and an artificial food (MicroMIN) between trials. The age of tested GF ranged from 15 to 27 days (standard length (SL) from 7.4 to 10.1 mm); BT ranged from 16 to 30 days (SL 5.2–7.5 mm). By the time of the experiments fish had developed a swimbladder (separated in two parts) and fins, explored actively the aquarium when hungry, they swam most of the time (up to 95%). Mean swimming speed was variable but not correlated with fish body length during this period. Water temperature was maintained between 19 and 22° C, and light intensity at the water surface was between 100 and 200 lux. All experiments were carried out between 1100 and 1700 h.

During the experiments with the food patches we used immobile particles (decapsulated cysts and nauplii of *Artemia* killed by heating) to maintain a relatively stable position and size of patches. Prior to the experiments, larvae were given experience with immobile food particles. About 1–1.5 weeks after hatching, both GF and BT readily ingested live *Artemia* nauplii. When presented with immobile prey most hungry larvae of both species at first rejected seized particles. After 1–3 days of preconditioning larvae began to ingest about 50–80% of seized particles. We started our experiments with larvae that achieved this state. GF larvae usually reached this state sooner than BT larvae.

When studying the swimming response of hungry larvae to consumption of individual food particles we used live *Artemia* nauplii as well as killed nauplii and decapsulated cysts. Food items were placed on the bottom of the observation tank in the form of square patches (4–9 cm^2) with a density of about 15 ind cm^{-2}, or as isolated items in the different parts of the aquarium.

At the start of each experiment 3 fish (to prevent abnormal behaviour due to isolation) were transferred to a square plastic aquarium (25 × 25 cm) with a water depth of 4 cm. Each such aquarium either contained food or was empty. All experiments were carried out with larvae starved for about 15 hours. During each observation the behaviour of only one fish was recorded. (The three larvae in aquarium differed slightly from each other in colour or size). It was obvious from pilot experiments that neither GF or BT larvae were disturbed by the presence of the observer sitting beside the observation tank. A grid with numbered 1 cm^2 squares was placed under the transparent bottom of the observation aquarium. The behaviour of the fish was recorded by direct observation using a multichannel recorder, a tape-recorder and a stop-watch. The position of a chosen fish was recorded every 5 s to allow the swimming speed, swimming path and frequency of visits to different parts of the aquarium to be calculated. This method does not yield an exact picture of a fish's movement because of underestimation of turns and speed changes within 5 s intervals and inside each of 1 cm^2 square, but it is quite adequate for describing swimming path characteristics and estimating swimming speed in different situations. For example, to compare mean swimming speeds of larvae in aquaria with food (Vf) and without food (Ve) we

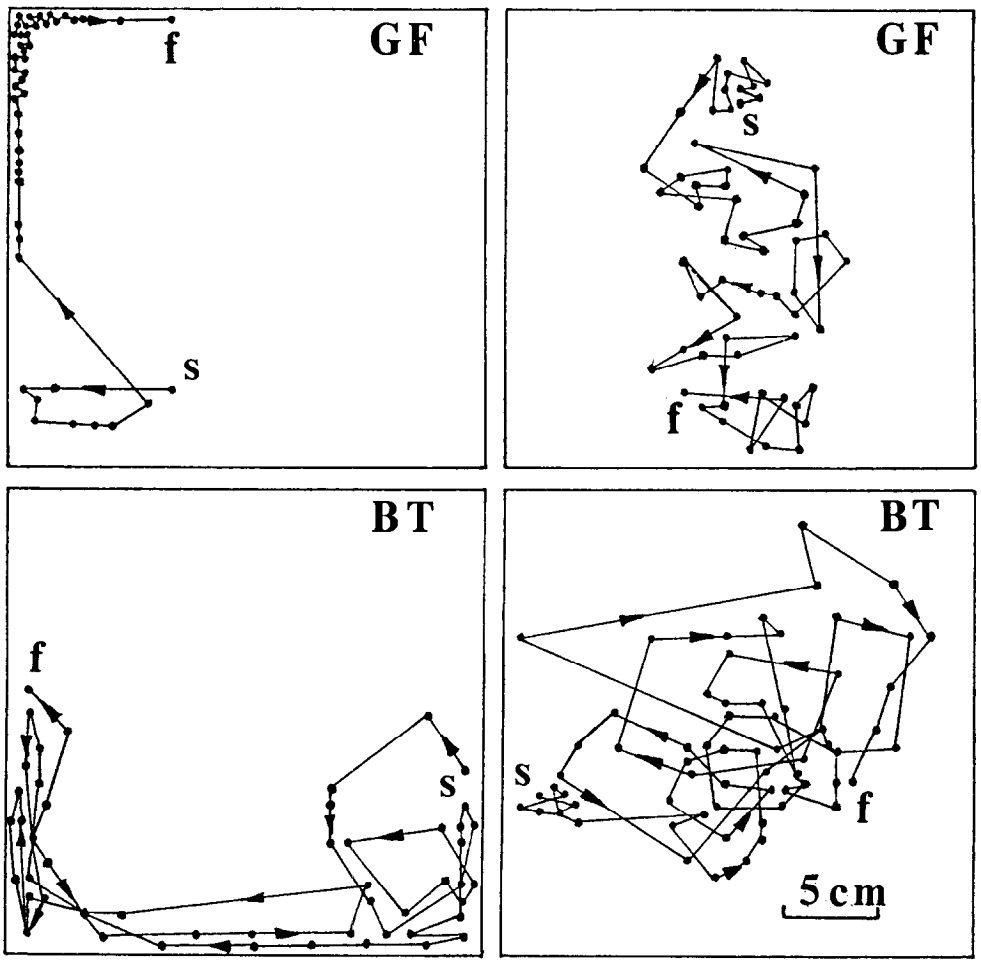

Fig. 1. The 5-min swimming paths of hungry GF (age 21 days) and BT (23 days) larvae before (left panel) and after (right panel) consumption of 2–3 artemia mauplii. S – beginning, F – end of record. The location where the food was consumed is just at the point of first recording in right panel (GF, BT).

calculated speed values in 1 s and 5 s intervals using videotape recordings. Comparing Vf/Ve ratios calculated using 1 s and 5 s intervals, we obtained values that differed by no more than 20%.

The differences in fish behaviour in the situations studied were estimated on the base of the mean swimming speed, frequency distribution of V values and frequencies of visits to different parts of the aquarium. One-way ANOVA was used to compare group means and Kolmogorov-Smirnov tests were used to compare frequency distribution of variables.

Results

Mean swimming speeds of fish larvae, the form of their swimming path and the frequency of visits to different parts of the aquarium were influenced by the presence and distribution of food and by the satiation level of the fish.

Interaction with an individual prey (or a small number of food particles – smaller than 5% of the number necessary to fill the digestive tract) influenced the movement characteristics of the hungry fish larvae. Each prey consumption was followed by a certain sequence of behaviours. The method of swimming path recording used here, makes it pos-

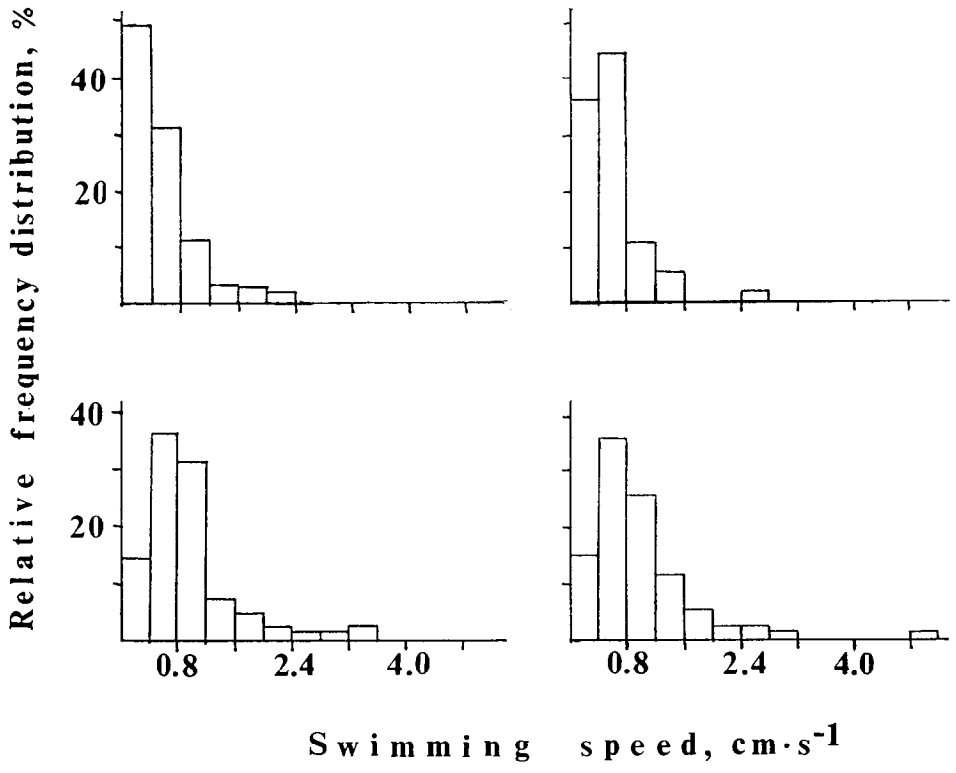

Fig. 2. Examples of frequency distributions of swimming speed values (V, cm · s^{-1}) of hungry GF larvae (age 21 days). Upper panel: 15 min records in aquarium without food. Lower panel: left – during 35 min of regular consumption of food items at 5 min intervals; right – 15 min following consumption of one food item.

sible to distinguish two movement modes: (1) slow swimming with short 'steps' (defined as the straight line between neighbouring turns) and large turn angles at the place where a food particle was consumed (the duration of this behaviour was not more than 1 min); (2) fast swimming with long 'steps' and large turn angles (this behaviour lasted from a few minutes to tens of minutes). Trajectories that illustrate the above swimming modes are shown in Figure 1 where two examples of 5 min observations of the swimming paths of hungry fish before (left) and after (right) food particle ingestion are given. Swimming speed (mean ± S.E.) of hungry GF larvae before encountering food (0.31 ± 0.01 cm · s^{-1}) was approximately half that during the fast swimming period after consumption of an individual food item (0.60 ± 0.05 cm · s^{-1}). The difference between these means is significant ($F = 31.53$; d.f. = 1, 8; $p < 0.01$). Overall differences between the swimming speeds of hungry fish larvae before and after prey consumption are clearly discriminated by comparing the frequency distributions of V values (Fig. 2). The difference between distributions is significant at $p < 0.01$ (Kolmogorov-Smirnov test).

When encounters of hungry larvae with food items were rare and approximately regular (every 5 min), larval swimming speed remained high for a relatively long time (about 35 min). The frequency distributions of V values for a hungry larva swimming in an aquarium without food and that at rare encounters of food items are significantly different ($p < 0.05$ Kolmogorov-Smirnov test) (Fig. 2).

Note that the fish swam mostly near the aquarium walls before prey were encountered; after a prey had been consumed the fish left the near wall zone for a long time (approximately 20–30 min) (Fig. 3). The frequency distribution histograms of locations obtained for the period preceding food consumption were distinctly positively skewed.

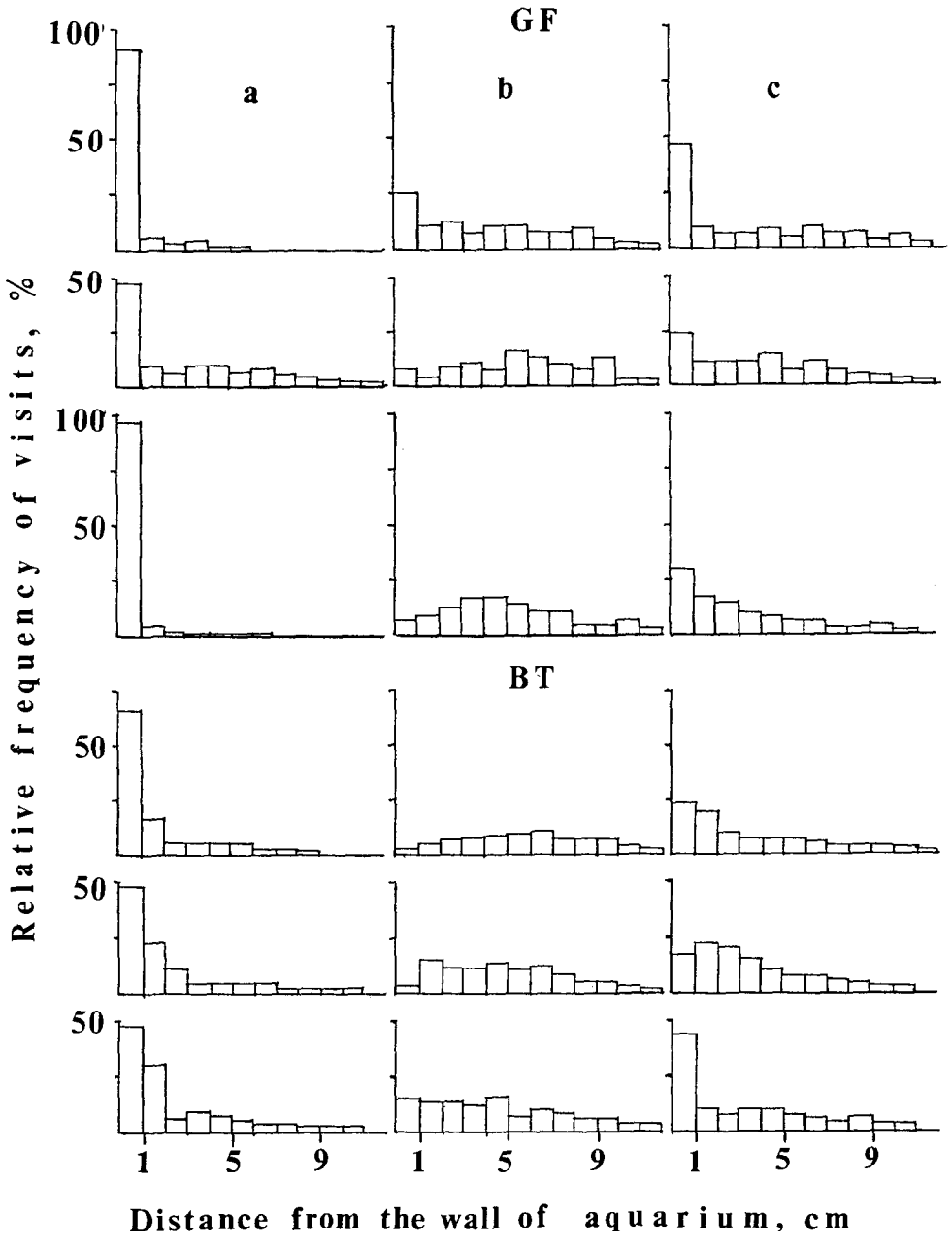

Fig. 3. The frequency of fish visits to 1 cm zones of 25 × 25 cm aquarium. Three upper rows of histograms – GF (age 22–23 days); lower – BT (23–25 days) larvae. In each row the results for one individual are presented: A – hungry fish before food consumption; B – first 15 min following consumption of some food items; C – the next 15 min period. The differences between frequency distributions for each A–B pair are significant (Kolomogorov-Smirnov test, $p < 0.01$). N (number of recorded fish positions) = 180 for each histogram.

They became more symmetrical for the 15 min period just after food consumption. The differences between these frequency distributions were highly significant in all cases (Kolmogorov-Smirnov test, $p < 0.01$). During the next 15 min after food consumption the distributions again became positively skewed. If another prey was not encountered for 30–60 min the initial highly asymmetrical distribu-

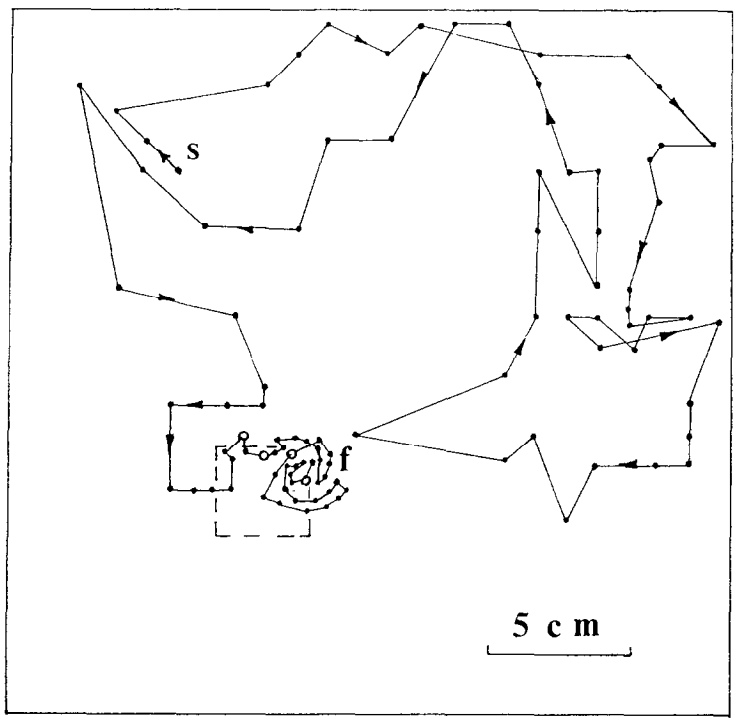

Fig. 4. A typical example of the swimming path of hungry GF larva (age 23 days) before and after encountering a food patch (broken-line square). Points – position of fish at 5 s intervals. Open circles – places where the fish stopped for more than 15 s. S – beginning; F – end of 5 min record.

tion was restored. In spite of some individual differences the pattern described was fairly general.

Having considered short-term changes in swimming characteristics we turn to long sequences of behavioural events. The most noticeable changes in swimming path were observed when hungry fish found a dense food patch. A typical example of a trajectory is shown in Fig. 4. After the fish entered the patch they moved considerably slower than before encountering the patch. For GF larvae swimming speed (mean ± S.D.) decreased from $0.42 \pm 0.04\,cm \cdot s^{-1}$ to $0.11 \pm 0.01\,cm \cdot s^{-1}$; for BT larvae from $0.42 \pm 0.03\,cm \cdot s^{-1}$ to $0.10 \pm 0.02\,cm \cdot s^{-1}$. The speeds of hungry larvae while searching and while foraging at the food patch are significantly different ($F = 62.59$ d.f. = 1,46, $p < 0.01$ for GF larvae and $F = 25.09$ d.f. 1,15, $p < 0.01$ for BT larvae).

After leaving the patch, satiated larvae moved at some intermediate speed ($0.27 \pm 0.02\,cm \cdot s^{-1}$ for GF and $0.27 \pm 0.02\,cm \cdot s^{-1}$ for BT larvae) for approximately 15–40 min. A larva was considered satiated when it consumed 10–30 (BT) or 20–50 (GF) food items (the maximal number which hungry larva consumed in a single feeding bout in our pilot experiments) and left the food patch for more than 30 min. This speed was higher than that in the food patch ($F = 65.7$; d.f. = 1,46; $p < 0.01$ for GF and $F = 16.1$; d.f. = 1,12; $p < 0.01$ for BT larvae) but slower than that during the search period ($F = 12.9$; d.f. = 1,46; $p < 0.01$ for GF and $F = 11.02$; d.f. = 1,12; $p < 0.01$ for BT larvae).

A comparison of the movement of larvae in the food patch with their movement between patches showed that in dense food patches fish swam more intermittently. Searching GF larvae made, on average 1.04 ± 0.28 stops per min, while foraging larvae made 2.75 ± 0.28 stops per min (the difference is significant; $F = 14.97$; d.f. = 1,8; $p < 0.01$). The mean duration of stops was longer in the case of foraging fish (10.6 ± 1.23 s versus 7.2 ± 0.75 s) but the difference was not significant. Similar results

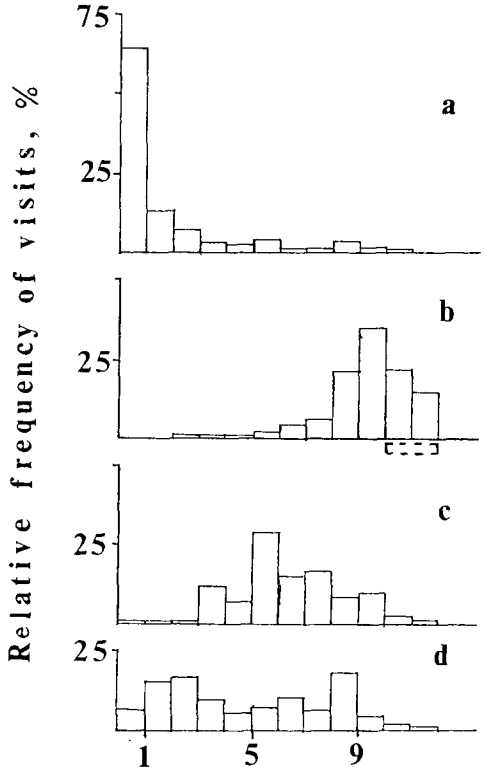

Fig. 5. The frequency of visits of BT larvae (age 25 days) to 1 cm zones of a 25 × 25 cm aquarium: a – hungry fish before encountering food patch, b – while foraging at the food patch (dashed rectangle), c – 1 hour, and d – 3 hours after consumption of all food items.

were obtained for BT larvae: stop frequencies were 1.64 ± 0.26 and 2.39 ± 0.10 per min (for search and foraging periods, respectively); the mean duration of stops was 9.13 ± 0.62 and 16.05 ± 5.2 s; but statistical analysis was not carried out because of the small number of observations.

The frequency of visits to the different parts of the aquarium before, during and after foraging are shown in Fig. 5. Mostly near-wall swimming during the search period was followed by practically exclusive visiting of the food patch and the nearby area while foraging. The initial 'near wall distribution' was restored only 5–6 hours after food patch consumption.

Discussion

Changes in animal movement just after prey consumption have repeatedly been demonstrated for different predators (Beukema 1968, Smith 1974, Thomas 1974, Waddington & Heinrich 1981, Evans & O'Brien 1986, Mikheev & Pakulska 1988). After consumption of a food object, the linear displacement of a threespined stickleback was smaller than during the search. The main cause of this effect was increased tortuosity of the swimming path after food consumption (Thomas 1974). In a detailed study on the planktivorous white crappie's movement while foraging (Evans & O'Brien 1986), swimming speed and time budget were recorded in a simple environment where only the predator's encounters with prey were taken into account, and the displacement of the fish relative to other environmental objects was ignored. Such an experiment imitates foraging in the pelagic environment. In our experiments we paid more attention to the mean swimming speed of foraging fish and characteristics of their swimming path in relation to spatially fixed objects (food particles, patches, aquarium walls). This situation resembles foraging in a structured and relatively stable benthic or inshore environment.

On the basis of the data presented in this paper and results published previously (Mikheev & Pakulska 1988) we recognize pattern of behavioural events that followed prey consumption by hungry fish larvae. Given very sparsely distributed food particles each ingestion is followed by the following behaviours: (1) cessation of swimming (this period lasts for a few seconds to tens of seconds, depending on relative prey size); (2) slow swimming with short steps close (not farther than 2–3 fish body lengths) to the place where the food particle was consumed (duration less than one minute); (3) fast swimming with relatively long 'steps' (lasting from a few minutes to tens of minutes). During the third period fish swam far from the walls, intensively visiting the central area of the aquarium. We have called this behaviour, which leads to an increase in the search rate, 'area increased searching'. The same behavioural effect of encountering prey by hungry fish larvae, i.e. sharp transition from explo-

ratory behaviour when fishes moved at rather high speed (about 1 body length · s^{-1}) mostly near the walls of the aquarium to foraging behaviour (low speed, tortuous swimming path far from the walls), was observed not only in GF and BT larvae but also in roach, *Rutilus rutilus,* larvae from a natural population (personal unpublished observations).

The period of immobility just after fish larvae seize a prey is likely to be caused by prey handling. The duration of stops was positively related with relative prey size (Mikheev & Pakulska 1988), and handling time increases with relative prey size (Werner 1974).

The behaviour following the handling pause resembles an 'area restricted searching' (Tinbergen et al. 1967), when the predator thoroughly searches the area close to the point of feeding. If another prey was not encountered the swimming speed of larvae increased and widening of the searching area took place. The sequence of these behavioural events was observed with both moving and immobile prey.

When the intervals between predator-prey encounters are large (several minutes) all three behaviours (pause, slow swimming and fast swimming) can be observed during an interval. In this case mean swimming speed is relatively high because of the significant contribution of fast swimming. The longer the intervals between prey encounters (low food density) the higher is the mean swimming speed of foraging fish. This relationship is probably valid at low prey densities (smaller than 10 ind · l^{-1}) as in the experiments with the herring larvae (Munk & Kiorboe 1985) and anchovy larvae (Hunter & Thomas 1974). At a higher food density, and relatively short intervals between successive prey consumptions, a fish encounters its next prey during the period of slow swimming (fast swimming does not occur). In this case, if the stops are short, the mean swimming speed of foraging fish approximates the slow swimming speed.

The most drastic change in swimming we observed was when fish encountered a food patch; this sharp transition was also recorded by Hunter & Thomas (1974). 'Area restricted searching', which we observed for the short period after consumption of a single prey, was also noted during fish foraging in a dense food patch. But in the latter case the larvae demonstrated such behaviour for a far longer time. It is worth mentioning that satiated larvae returned to the area where the food patch had previously been for approximately one hour after patch consumption. It is remarkable that the GF larvae leaving the food patch came back for the next time moving along the more straight trajectory (unpublished data). These results indicate the importance of learning when the positions of food patches are stable. Older goldfish effectively use local landmarks during exploratory and foraging behaviour (Warburton 1990).

Low swimming speed and a tortuous swimming path, as well as relatively frequent stops, characterized movement within the food patch. According to our observations, some stops (especially at the beginning of a foraging period) were not caused by food handling. Fish can search for prey during the pauses in movement (O'Brien et al. 1986, Evans & O'Brien 1986, O'Brien et al. 1989). Other hypotheses in this case probably are 'confusion effect' (Miller 1922, Welty 1934) or 'sensory overload' (Marcotte & Browman 1986, Milinski 1990) causing the foraging predator to become less efficient.

According to theoretical considerations (Ware 1975), the relation between optimal swimming speed and food concentration is described by the bell-shaped curve when maximizing growth is taken as the performance criterion. In the range of low food concentrations swimming speed increases with prey density. However, experimental data (Hunter & Thomas 1974, Munk & Kiorboe 1985, our data) show a decrease of swimming speed with an increase of prey density. The discrepancy between theoretically expected swimming speeds and those found experimentally has been probably caused by different time scales. Ware's (1975) analysis is based on a relatively long time period during which growing fish balanced their energy costs and gains. During this period, a foraging fish adopts its swimming speed to maximize its growth rate at an evenly distributed food supply. In the case of the above mentioned experiments relatively short-term behavioural responses were under consideration. Such responses could increase the efficiency of search for food in a patchy environment, in-

ducing 'area increased searching' (high swimming speed) when prey are sparsely distributed, and 'area restricted searching' (low swimming speed) when the fish forage in a food patch.

To use the mean swimming speed as a variable in behavioural models (e.g. Rashevsky 1959, Dabrovski et al. 1988), or to estimate the volume of water searched (search rate) (Rosenthal & Hempel 1970, Blaxter & Staines 1971, Houde & Schekter 1980, Munk & Kiorboe 1985), one should take into account the fact that swimming speed depends on food density. Over a broad range of 'intermediate' densities, mean swimming speed is relatively constant. At 'low' densities the speed increases because of 'area increased searching', while the decrease of mean swimming speed at dense food patches is caused not only by swimming responses to prey consumption but probably also by 'sensory overload' due to the necessity of processing too much information.

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