Factors affecting prey selection by young bream *Abramis brama* and roach *Rutilus rutilus*: insights provided by parallel studies in laboratory and field

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Synopsis

Prey selection by underyearling bream and roach was studied in both the laboratory and field. When presented with cladoceran and a more elusive copepod prey both fish species select against copepods, regardless of the relative prey sizes. However, the field diet of bream, but not roach, consistently includes a large proportion of copepods. The explanation for this discrepancy lies in the timing and location of foraging in the field. Bream foraging, unlike that of roach, is largely restricted to the hours of darkness and to the lowest stratum of the lake. The Microcrustacea of this stratum is depleted of cladocerans at night, because of vertical migration, and is relatively rich in copepods.

Introduction

There is much interest in prey choice in predator-prey interactions (Charnov 1976, Krebs et al. 1977, Pyke et al. 1977, Townsend & Hughes 1981), including fish-zooplankton interactions (O'Brien 1979, Mittelbach 1981, Milinski 1984, Townsend & Winfield 1985). Recent work has demonstrated the value of performing parallel studies in laboratory and field (e.g. Winfield et al. 1983, Werner 1984). Although earlier laboratory results allowed us to predict correctly the natural diet of roach, *Rutilus rutilus* (L.), they could not explain the diet of bream, *Abramis brama* (L.), in Alderfen Broad. We hypothesised (Winfield et al. 1983) that size-selective predation or subtle differences in the location and timing of foraging may be responsible for the observed discrepancies.

The present paper reports the results of lab-oratory and field tests of the above hypotheses. We extend our laboratory experiments to include the simultaneous presentation of different prey types and sizes, and make more detailed observations of the distributions of foraging bream, roach and their prey under natural conditions.

Methods

Laboratory studies

1. Simultaneous presentation of two prey types. The experimental protocol involved in the simultaneous presentation of the contrasting prey types closely followed that used in our earlier work with monospecific prey (Winfield et al. 1983). The fish used in the experiments (55 to 60 mm in total length, TL) were collected from Alderfen Broad,

U.K. (National Grid ref. TG 354 196) and held in aquaria at $14 \pm 2°$ C on a diet of commercial pellet food for several weeks before use. The prey types used were the cladoceran *Daphnia magna* Straus (size range 1.50–1.80 mm excluding the caudal spine) obtained from laboratory culture, and the copepod *Cyclops vicinus* (size range 1.50–1.80 mm excluding the caudal setae) collected from the pelagic zone of Alderfen Broad. Pilot studies using bream had shown that laboratory-cultured *D. magna* provided an acceptable substitute for the seasonally-scarce *D. hyalina* of Alderfen Broad. Both daphnids are identical in escape ability and, in common with *C. vicinus*, elicit reaction distances of 50 mm or less under the conditions of our experimental arenas (Winfield 1983).

Experiments were conducted in 10 l aquaria at $14 \pm 2°$ C and under light levels of approximately 1000 lx (measured with a Lambda Instrument Corporation Model LI-185 photometer). An individual fish, maintained in the absence of zooplankton for a minimum of seven days, was introduced to the arena at least 90 min before observation commenced. At the end of this period 20 cladocerans and 20 copepods were introduced, and the behaviour of the fish was recorded for 15 min. At the end of each trial the fish was removed and kept isolated with an excess of food pellets for 24 h, after which the procedure was repeated for a series of five days. A total of eight replicates was performed on each day. The concentration of prey (4 individuals l^{-1}), although four times greater than that of the earlier studies, remains far below levels commonly encountered in nature, and we consider confusion effects to be unlikely.

Nine behavioural units were defined and the occurrences of these were recorded as they were exhibited by the fish, in addition to the identity of the prey type under attack. Only attacks on prey which were out of contact with the sides or bottom of the arena were included in this analysis.

Approach. The fish makes its approach with its eyes directed at the prey item.

Chase. The fish follows a prey item as it moves away.

Unsuccessful strike. The fish simultaneously sucks and lunges at the prey but fails to make physical contact.

Successful strike. As above, but contact is successfully made.

Capture. The prey item is taken completely inside the fish's mouth.

Emergence. The prey comes out of the mouth. This may be due to the prey escaping or the predator actively ejecting it.

Mastication. The fish exhibits buccal and opercular movements characteristic of mastication.

Swallow. This is assumed to have occurred when mastication ceases and the prey has not emerged.

End of attack. The fish ceases attacking a particular prey item, or a captured prey is swallowed.

Laboratory studies of prey selection are always susceptible to the complicating effects of prey depletion. This study was no exception as relatively low initial prey densities were essential for the observer to record accurately and reliably the outcome of each attack, and replacement of prey as they were consumed was not possible as pilot studies revealed that this procedure would have alarmed the fish. To reduce the effects of differential prey depletion, analyses of selection patterns only consider data from attacks carried out before and including the consumption of the tenth prey item. Thus prey depletion was at most 25% (not all fish consumed ten or more prey in each trial), although the distribution of this impact was not the same on the two populations and, by definition, was heavier on the preferred prey. The net effect of this will be to underestimate the predators' preferences as the favoured prey will become increasingly rarer as the trial progresses. Analyses of attack efficiencies and attack patterns consider all data obtained, including those relating to the eleventh and subsequent prey. Prey choice and predator attack efficiency were not affected by satiation during the course of a trial as the number of prey available was designed to be well below potential satiation levels.

2. Relative sizes of prey types. Ten experimental arenas consisted of white translucent plastic containers 200 mm in diameter, 140 mm deep, containing 2 l of water. The top of each arena was covered by a lid with a small ($2 \, cm^2$) central aperture. Temperature and light conditions were as above.

An individual fish (bream or roach; 55–60 mm TL) was introduced to the arena at least 90 min before 10 individuals each of two prey types were introduced through the aperture of the lid. The fish was allowed to feed for 30 min before being removed and kept alone with an excess of food pellets for 24 h, after which the procedure was repeated for a series of five days. The prey remaining in the arena at the end of each trial were identified and counted.

The two prey types used were 1.50–1.80 mm *Cyclops vicinus* and one of the following four categories of Cladocera: 0.30–0.44 mm *Bosmina longirostris* (Muller), 0.68–0.98 mm *Daphnia magna,* 1.50–1.80 mm *Daphnia magna* and 2.21–2.41 mm *Daphnia magna.* The copepods and *Bosmina* were obtained from Alderfen Broad while the various sizes of *Daphnia* were taken from a laboratory culture. Previous observations had shown bream and roach attack patterns on *Bosmina* to be similar to those shown on small daphnids (Winfield 1983). Copepods were thus presented to the fish together with cladocerans of size equal to approximately 22, 50, 100 and 137% of their own body lengths (equivalent to biomass ratios of approximately 5, 29, 138 and 295% (from length – dry weight regressions of Dumont et al. 1975).

Ten replicates of each predator-copepod-cladoceran combination were performed each day with the exception of bream feeding on copepods and *Bosmina* when, due to a scarcity of available bream, only four replicates were made. These experiments also suffered from the effects of prey depletion.

Field studies

1. Diet and electivity in the natural habitat. Ten bream (54–64 mm TL) and ten roach (51–54 mm TL) were collected from Alderfen Broad by electrofishing around noon on the 11 May, 1982, and again, ten bream (82–88 mm TL) and ten roach (69–74 mm TL) on the 28 June, 1982. Following preservation in 4% formalin, gut contents were examined and prey assigned to the classes: planktonic Cladocera, non-planktonic Cladocera and Copepoda (Winfield et al. 1983). In addition, measurements were made of the body lengths (excluding caudal spines or setae) of the dominant Microcrustacea in the fishes' diets (50 copepods from bream and 50 planktonic cladocerans from roach in May, and 50 copepods and 50 planktonic cladocerans from bream and 50 planktonic cladocerans from roach in June). The zooplankton available in the pelagic zone of Alderfen Broad was also monitored on these occasions using a Clarke-Bumpus sampler (volume filtered 100–200 l on each occasion), including measurements of body size (50 individuals of each prey type).

2. Timing and location of foraging. Between the 11 and 14 May 1982, four monofilament gillnets (two of bar mesh size 8 mm, and two of bar mesh size 6.25 mm), each measuring 10 m long by 1 m deep, were set in two pairs. One of each pair was set in the littoral zone of the lake perpendicular to an extensive reedbed (*Typha angustifolia* L. and *Phragmites australis* (Cav.) Trin. ex Steud) which fringed the east shore of the lake, while the other member of each pair was set parallel to the bank in the limnetic zone 35 m from the reedbed (width of the lake approximately 150 m). Thus the water columns of both the littoral and limnetic zones of the lake were sampled (the water depth in these areas varied between 0.80 and 1.10 m). Each net was notionally divided into 26 columns (each approximately 38 cm wide, corresponding to the distance between successive floats) and 5 rows (each approximately 20 cm deep) to allow the position of each captured fish to be recorded. The gillnets were set over a series of three 24 h periods, from dusk of day 1 to dusk of day 4. Each 24 h period was covered by two sets: a 'day' set running from immediately after dawn until immediately prior to dusk (approximately 16 h), and a 'night' set covering the remainder of the 24 h period, and including dusk and dawn.

Between the 10 and 11 June 1982, a series of 8 mm bar mesh size gillnet sets (the fish in the lake were now too large to be retained by the 6.25 mm nets) was made in conjunction with a microcrustacean sampling exercise described below. Nets were positioned as in May, but for only 30 min, repeated at approximately 4 h intervals over this single 24 h

period. The identity and location of each captured fish were recorded.

3. Diel changes in prey microdistributions. Diel changes in microcrustacean vertical distributions were monitored at Alderfen Broad between the 10 and 11 June 1982. A vertical series of samples (at depths of approximately 5, 35, 65 and 75 cm (i.e. bottom of the water column) was taken from near the limnetic gillnet at 4 h intervals over the 24 h period, using a 12 volt D.C. electric water pump which filtered 3 l of water through a 45 μm zooplankton mesh on each occasion. A Clarke-Bumpus sample was also taken from this site near midday on the 10th. Samples were preserved in 4% formalin and subsequently examined under a binocular microscope.

Results

Laboratory studies

1. Simultaneous presentation of two prey types. Although both *Daphnia* and *Cyclops* elicit similar reaction distances they are not equally conspicuous because copepods, but not *Daphnia*, tend to rest motionless on the sides and bottom of the arena (Winfield 1983). Nevertheless, this effect will be the same for bream and roach and hence will not result in any differences in selection patterns between the two predators. At any one time, under the conditions of our experimental arenas only approximately 25% of a *Cyclops* population in the presence of a predator is actively swimming in the water column (Winfield & Townsend 1983), leading us to expect a non-discriminating predator to allocate 20% (i.e. 25/125) of its attacks towards the copepods.

Initially, neither bream nor roach deviated significantly from the 20% of attacks at *Cyclops* (Fig. 1) [t tests comparing mean of day 1 with expected value of 20%: bream, $18.06 \pm 2.09\%$ (mean ± 1 S.E.), $t = 0.352$, $df = 6$, $p > 0.10$; roach, $16.16 \pm 1.98\%$, $t = 0.794$, $df = 5$, $p > 0.10$]. Thus initial selection against copepods was similar for bream and roach (t test on means of day 1: $t = 0.254$, $df = 11$, $p > 0.10$), a similarity which also
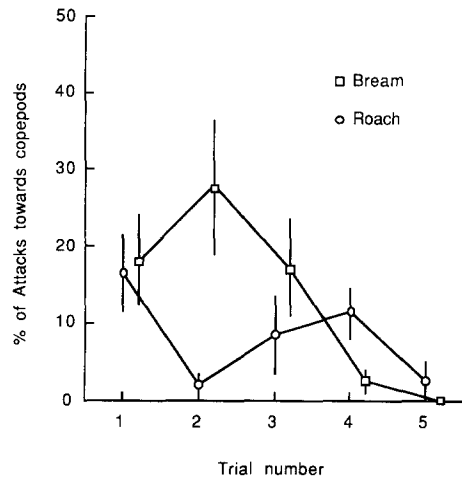

Fig. 1. The effect of increasing experience on the percentage of attacks directed towards *Cyclops* by bream and roach when it is presented together with *Daphnia* (mean ± 1 S.E.). Bream are represented by squares and roach by circles.

prevailed on the last day of trials (t test on means of day 5: $t = 1.00$, $df = 12$, $p > 0.10$). However, during the series of trials both predators increased their selection against the copepods (single-classification ANOVA: bream, $F = 5.124$, $p < 0.01$; roach, $F = 2.831$, $p < 0.05$), with the result that both fish eventually had fewer *Cyclops* in their diets than would be expected of a non-discriminating predator (t tests comparing mean of day 5 with expected value of 20%: bream, $0.00 \pm 0.00\%$ (mean ± 1 S.E.), $t = \infty$, $df = 6$, $p < 0.001$; roach, $2.38 \pm 2.38\%$, $t = 7.398$, $df = 6$, $p < 0.001$).

Figure 2 shows the attack efficiency (the number of swallows as a percentage of the number of attacks) by bream and roach towards *Daphnia* and *Cyclops* during both the present mixed-prey experiments, and the earlier trials when the prey types were presented alone (data taken from Winfield et al. 1983). Mean attack efficiencies on *Daphnia* were always very high (range 70.00–100.00%), and did not vary significantly with predator type, treatment, or experience (e.g. single-classification ANOVA: bream on *Daphnia* alone, $F = 1.516$, $p > 0.10$; bream on *Daphnia* with *Cyclops* present, $F = 1.068$, $p < 0.10$; roach on *Daphnia* alone, $F = 0.489$, $p > 0.10$; roach on *Daphnia* with *Cyclops* present, $F = 0.769$, $p > 0.10$).

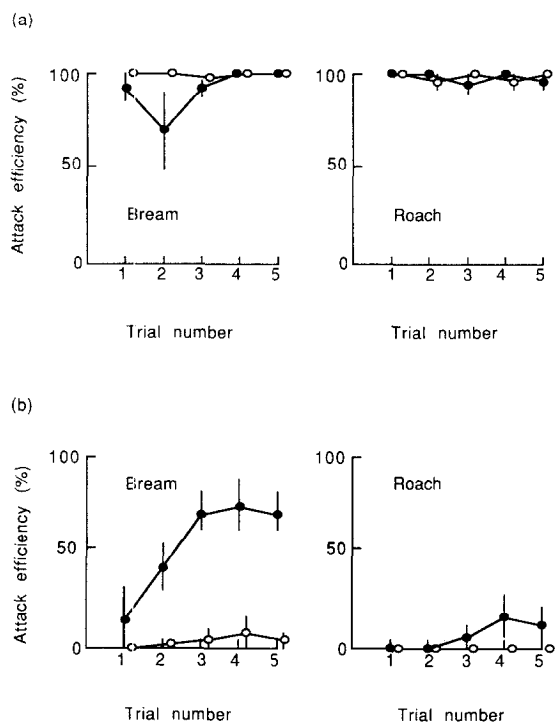Mean attack efficiencies on *Cyclops* showed

Fig. 2. The effect of increasing experience on the attack efficiency of bream and roach on (a) *Daphnia* and (b) *Cyclops* when the prey types are presented alone (closed symbols, data from Winfield et al. 1983), and when presented together (open symbols).
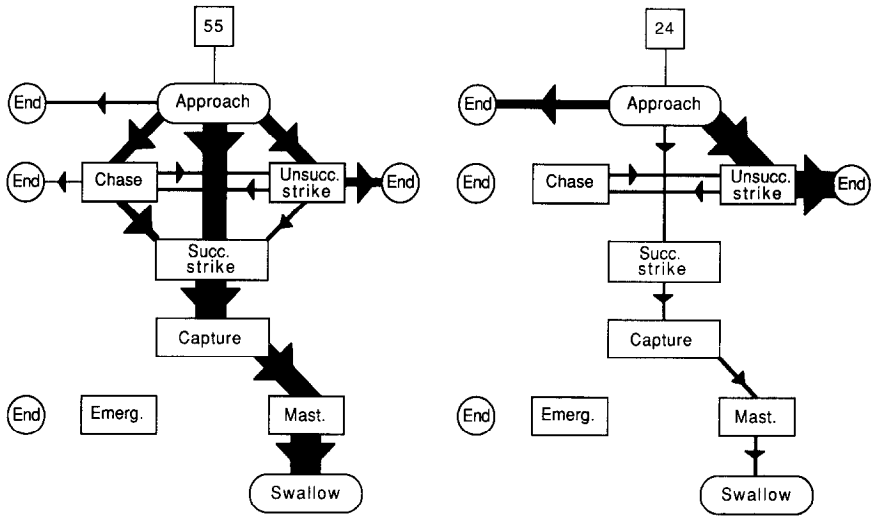
more variation (range 0.00–75.35%) dependent on predator type, treatment and experience. When *Cyclops* was presented alone, both predators showed initially low attack efficiencies which for bream, but not roach, increased significantly with experience (single-classification ANOVA: bream, $F = 3.219$, $p<0.05$; roach, $F = 1.409$, $p>0.10$). When *Cyclops* was presented together with *Daphnia* both predators again showed initially low attack efficiencies which, with the cladocerans present, did not increase significantly with experience in either fish (single-classification ANOVA: bream, $F = 0.725$, $p>0.10$; roach, $F = 0.00$, $p>0.10$). When copepods were presented alone, the ultimate attack efficiency of bream was significantly greater than that of roach (t test comparing means of pooled data from days 4 and 5: $t = 4.577$, $df = 21$, $p<0.001$), but this was not the case when the cladoceran was present ($t = 1.695$, $df = 11$, $p>0.10$). The final attack efficiencies of both pred-

ators on the elusive copepod prey were significantly lower when they were presented in combination with the more easily captured cladocerans (t test comparing means of pooled data from days 4 and 5 when cladoceran absent and present: bream, $73.48 \pm 30.64\%$ (mean ± 1 S.E.) against $4.86 \pm 3.12\%$, $t = 5.346$, $df = 20$, $p<0.001$; roach, $15.90 \pm 7.07\%$ against $0.00 \pm 0.00\%$, $t = 2.249$, $df = 12$, $p<0.05$).

The reasons behind this dramatic decrease in attack efficiency on *Cyclops* are revealed by further consideration of the data. Firstly, it may be noted that the decrease was not simply a result of the fish feeding on the mixed prey having had less practice on the copepods: the numbers of attacks on *Cyclops* before the 'experienced' attack efficiencies were reached (i.e. attacks made in trials 1 to 3 inclusive) were not significantly different between the treatments for either predator (G test, Sokal & Rohlf 1981, on number of attacks on copepods during first three trials when they were presented alone compared with when they were presented together with the cladocerans: bream, 75 against 74, $G = 0.007$, $p>0.10$; roach, 51 against 69, $G = 2.71$, $p>0.10$).

The attack patterns of bream and roach feeding on *Cyclops* during their final two trials (i.e. days 4 and 5, data pooled because of relative rarity of attacks against copepods when cladocerans present) are shown in Figure 3. The nine behavioural units are arranged as a flow chart to illustrate the relative frequencies of the behavioural transitions. The reduction in attack efficiency towards *Cyclops* in mixed prey experiments is not the result of relatively more attacks being aborted immediately after the fish's initial approach and prey identification (G test on proportion of attacks ended immediately after initial approach when copepods presented alone compared with when presented together with cladocerans: bream, $3/55 = 5\%$ against $5/24 = 21\%$, $G = 3.664$, $0.10 >p>0.05$; roach, $8/50 = 16\%$ against $5/21 = 24\%$, $G = 0.553$, $p>0.10$). Similarly, the proportion of chases followed by a strike was uniformly high among fish and treatments (G test on proportion of chases leading to a strike when copepods presented alone compared with when presented together with cla-
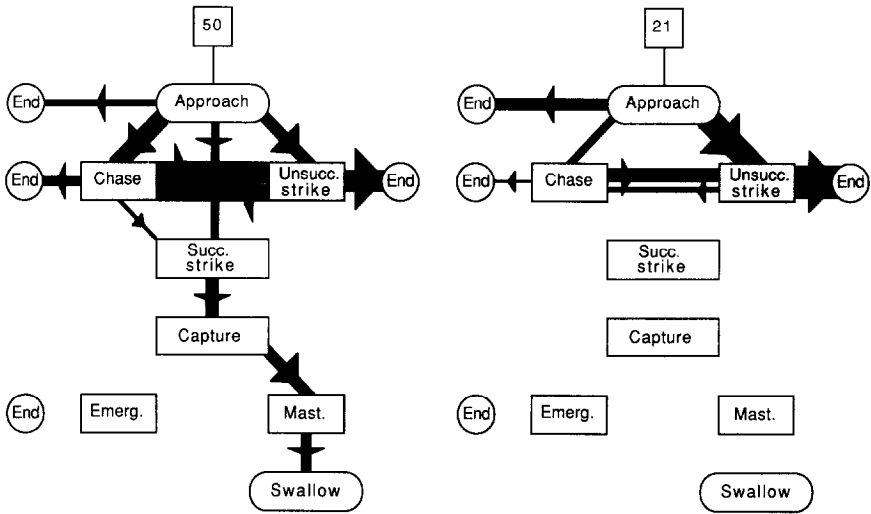
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(a) Bream

55

End ← Approach
End ← Chase — Unsucc. strike → End
Succ. strike
Capture
End   Emerg.   Mast.
Swallow

Cyclops presented alone

24

End ← Approach
End   Chase — Unsucc. strike → End
Succ. strike
Capture
End   Emerg.   Mast.
Swallow

Cyclops presented with *Daphnia*

(b) Roach

50

End ← Approach
End ← Chase — Unsucc. strike → End
Succ. strike
Capture
End   Emerg.   Mast.
Swallow

Cyclops presented alone

21

End ← Approach
End ← Chase — Unsucc. strike → End
Succ. strike
Capture
End   Emerg.   Mast.
Swallow

Cyclops presented with *Daphnia*

Fig. 3. Flow charts showing the attack pattern of (a) bream and (b) roach against *Cyclops* presented alone (data from Winfield et al. 1983) and *Cyclops* presented together with *Daphnia*. All charts show data combined from days 4 and 5 of the respective experiments. The units are joined together by lines of width proportional to the frequency with which that transition was exhibited by the fish. Arrow-heads show the direction of each transition. The number of approaches observed is shown at the top of each flow chart.

docerans: bream, 15/16 = 94% against 2/2 = 100%, G = 0.243, p>0.10; roach, 31/41 = 76% against 5/6 = 83%, G = 0.186, p>0.10). However, differences were observed in strike efficiency: for bream this parameter decreased significantly from 38/61 = 62% to 2/21 = 10% when the copepods were presented together with cladocerans (G = 19.086, p<0.001) and for roach from 9/52 = 17% to 0/18 = 0% (G = 5.797, p<0.05). Finally, both predators showed significantly fewer chases when the alternative cladoceran prey was present (G test on proportion of attacks involving chases when copepods presented alone compared with when presented together with cladocerans: bream, 12/55 = 22% against 1/24 = 4%, G = 4.412, p<0.05; roach, 26/50 = 52% against 5/21 = 24%, G = 4.863, p<0.05).

In contrast to the above, almost all attacks by both species on *Daphnia* during their final two trials followed the simplest sequence possible: approach, successful strike, capture, masticate, swallow. Chases were extremely rare (2 in a total of 444 attacks), as were unsuccessful strikes (3 in a total of 458 strikes). Both fish were very efficient predators of cladocerans under both prey regimes.

2. Relative sizes of prey types. The abundance of *Cyclops* in the diet of roach did not differ significantly over the range of body sizes of the alternative cladoceran prey (Fig. 4), but a significant change was shown by the bream (data taken from the last two trials) (single-classification ANOVA: roach, F = 0.065, p>0.10; bream, F = 3.873, p<0.05). Further analysis of the bream data by the Tukey-Kramer method (Sokal & Rohlf 1981) revealed that bream took significantly fewer copepods when these prey were presented together with the largest size class of cladocerans (Table 1). Overall, copepods were relatively less abundant in the diet of roach compared with bream (t test on data pooled from all cladoceran size classes: bream, 15.63 ± 1.67% (mean ± 1 S.E.) against roach, 4.14 ± 0.98%, t = 5.92, df = 127, p<0.001).
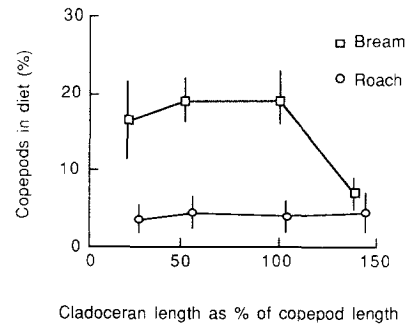

Fig. 4. The effect of relative prey size on the contribution of *Cyclops* to the diets of bream and roach when it is presented together with an equal number of cladocerans (mean ± 1 S.E.). Bream are represented by squares and roach by circles.

Field studies

1. Diet and electivity. Figure 5 shows the composition of available prey (as assessed by the Clarke-Bumpus sampler) and the diets of bream and roach in May and June of 1982. In May, under the prevailing conditions of prey abundance (individuals l^{-1}: Copepoda 52, non-planktonic Cladocera 1, planktonic Cladocera 43), 90.2% of bream diet was composed of copepods while planktonic cladocerans made up 95.0% of the diet of roach. In June, copepods were less and planktonic cladocerans more abundant in the environment (individuals l^{-1}: Copepoda 12, non-planktonic Cladocera 0, planktonic Cladocera 792), and reflecting this, copepods declined slightly to constitute 73.1% of bream diet

Table 1. Results of examination of the pattern of copepod contribution to the diet of bream by the Tukey-Kramer method. Cladoceran classes (large, *Bosmina*, small, medium) are ranked in ascending order of importance of co-presented *Cyclops* in the diet. Modulii of differences between pairs of means are given below the diagonal, and corresponding minimum significant differences are given above the diagonal. Differences larger in absolute value than their MSD value are significant at the 0.05 level and are marked with an asterisk.

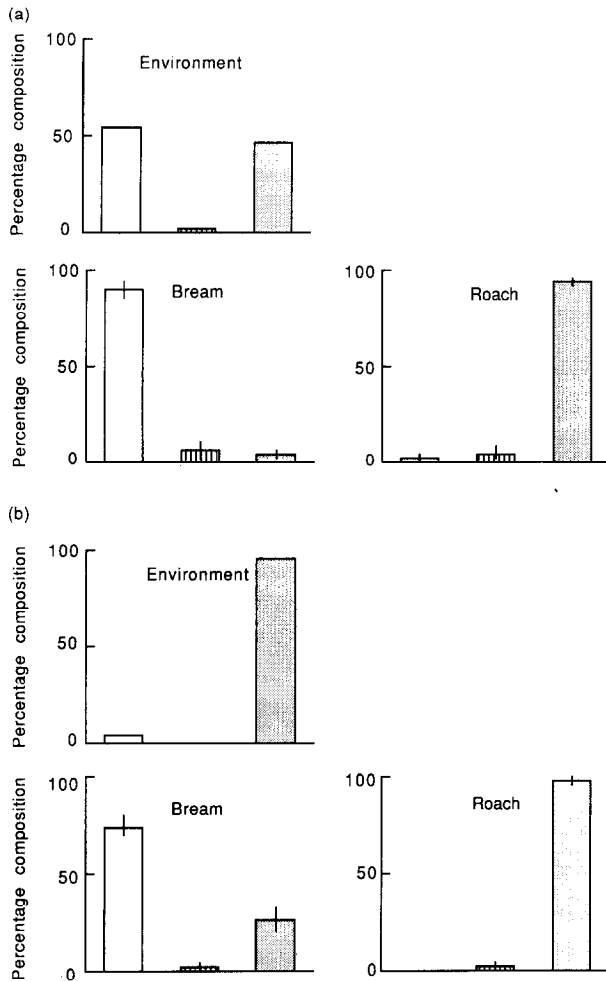|	large	*Bosmina*	small	medium
large	–	3.936	3.105	3.065
Bosmina	9.66*	–	3.901	3.869
small	12.21*	2.55	–	3.019
medium	12.30*	2.64	0.09	–

(a)

(b)

Fig. 5. Compositions of Microcrustacea in the environment and diets of bream and roach in (a) May and (b) June 1982. Prey items are divided into three groups: Copepoda (open bar), non-planktonic Cladocera (shaded bar) and planktonic Cladocera (stippled bar). Means ± 1 S.E. are shown for the data on fish diet.

icantly larger than the mean size of non-planktonic cladocerans when they were present (t test: May, t = 3.73, df = 98, p<0.001). In both months, the principal component of bream diet (Copepoda) was significantly larger than that of roach (planktonic Cladocera) (t test: May, t = 16.15, df = 98, p<0.001; June, t = 26.83, df = 98, p<0.001).

2. Timing and location of foraging. The May gillnet samples captured 76 bream (45–66 mm TL) and 92 roach (43–66 mm TL), while those of June caught 7 bream (56–70 mm TL) and 130 roach (56–70 mm TL). The change in relative catch sizes results from size-selectivity of the nets and differential growth rates and hence length frequency distributions of the two fish. Overall, bream were caught at a significantly greater rate (catch-per-unit-effort) at night than during the day on both occasions (Table 3, t test: May, t = 3.369, df = 22, p<0.01; June, t = 2.863, df = 12, p<0.05). In contrast, equivalent catch rates of roach did not differ significantly (t test: May, t = 1.764, df = 22, 0.10 >p>0.05; June, t = 0.797, df = 12, p>0.10).

In May, most individuals of both species were caught in the littoral net, but this pattern was not statistically significant for bream (proportion of total bream day catch taken in the littoral nets: 6/9 = 67%). The pattern was significant for roach (G test on proportion of total roach day catch taken in the littoral nets: 29/41 = 71%, G = 7.266, p<0.01). In June, bream were absent from both day nets but roach again showed the same significant pattern (G test on proportion of total roach day catch taken in the littoral net: 40/61 = 66%, G = 6.018, p<0.05).

In contrast to the pattern observed during the day, roach were caught in statistically-similar numbers in the littoral and limnetic nets at night (G test on proportion of total roach night catch taken in the littoral net: May, 21/51 = 41%, G = 1.597, p>0.10; June, 28/69 = 41%, G = 2.464, p>0.10). On both occasions, night-time catches of bream were higher in the limnetic nets, but significantly so only for the May sample as the June nets produced only 7 bream (G test on proportion of total bream night catch taken in the littoral nets: May, 19/67 = 28%, G = 12.977, p<0.001; June 6/7 = 86%).

There were no significant differences between

which now contained an increased proportion of planktonic cladocerans (26.3%). The diet of roach remained dominated by planktonic cladocerans (99.9%). Non-planktonic cladocerans, which were rare in the environment in both May and June (1 and 0 individuals l^{-1} respectively), never comprised more than 6.1% of the diet of either fish.

In both May and June, the mean body size of copepods in the environment was significantly larger than that of planktonic cladocerans (Table 2, t test: May, t = 12.94, df = 98, p<0.001; June, t = 13.11, df = 98, p<0.001) which in turn was signif-

the mean depths of bream and roach caught during any comparable periods in the entire study (t test on mean depth of capture of bream and roach respectively: May day, 67.78 ± 6.19 cm (mean ± 1 S.E.) against 61.71 ± 2.61 cm, t = 0.904, df = 48, p>0.10; May night, 50.30 ± 2.23 cm against 46.67 ± 3.00 cm, t = 1.024, p>0.10; June day, no bream captured and so no comparison possible; June night, 67.14 ± 6.80 cm against 65.38 ± 2.23 cm, t = 0.249, p>0.10). Finally, for both fish and for both months, individuals were taken at deeper positions during the day than they were at night (t test on mean depth of capture in day and night sets respectively: May bream, 67.78 ± 6.19 cm against 50.30 ± 2.23 cm, t = 2.658, df = 74, p<0.05; May roach, 61.71 ± 2.61 cm against 46.47 ± 3.00 cm, t = 3.831, df = 90, p<0.001; June bream, no individuals captured during the day and so no comparison possible; June roach, 73.28 ± 1.94 cm against 65.36 ± 2.23 cm, t = 2.681, df = 128, p<0.01).

3. *Diel changes in prey microdistributions.* Copepods were found throughout the water column at all times, although always with greatest abundance just above the bottom sediments (up to 1920 individuals l^{-1}), and did not undergo any significant diel vertical migration (Fig. 6). Non-planktonic Cladocera were almost entirely restricted to the bottom of the lake (up to 213 individuals l^{-1}) although a very few were present in the water column itself, particularly during the night and dawn periods (up to 6 individuals l^{-1}). Planktonic cladocerans were consistently found throughout the water column but their abundance at the different depths varied considerably: this prey type underwent a marked upward vertical migration at night resulting in densities of up to 1644 individuals l^{-1} at the surface but relatively fewer (down to 158 individuals l^{-1}) near the bottom of the water column at this time.

The effects of these distributions and migrations on the microcrustacean community composition at different depths throughout the 24 h period are shown in Figure 6 which, for comparison, also shows the available prey composition as indicated by the Clarke-Bumpus sample (which produced densities of 187, 0 and 420 individuals l^{-1} for Copepoda, non-planktonic Cladocera and planktonic Cladocera, respectively). Two points should be noted. Firstly, planktonic cladocerans (overwhelmingly dominated by *Bosmina* in these samples) were generally by far the most abundant

Table 2. Body sizes (μm, mean ± 1 S.E.) of non-planktonic Cladocera (non-pl Clad), planktonic Cladocera (pl Clad) and Copepoda in the environment, and Copepoda in the diet of bream (Br Cop) and planktonic Cladocera in the diet of roach (Ro pl Clad), in May and June.

	pl Clad	non-pl Clad	Copepoda	Br Cop	Ro pl Clad
May	0.324±0.007	0.284±0.008	0.760±0.033	0.780±0.033	0.387±0.007
June	0.307±0.007	absent	0.926±0.047	1.085±0.028	0.312±0.007

Table 3. Catch-per-unit-effort (individuals h-1, mean ± 1 S.E.) of bream and roach during the day and night gillnet sets of May and June.

	Bream		Roach	
	day	night	day	night
May	0.05±0.02	0.70±0.19	0.21±0.08	0.53±0.17
June	0.00±0.00	2.33±0.95	15.12±5.07	23.00±9.03

a

Copepoda

depth (cm)
5
75

1200 2400 1200

Non-planktonic Cladocera

depth (cm)
5
75

1200 2400 1200

Planktonic Cladocera

depth (cm)
5
75

1200 2400 1200

Time of day

0 100
% of total population

b

C/B sample

depth (cm)
5
35
65
75

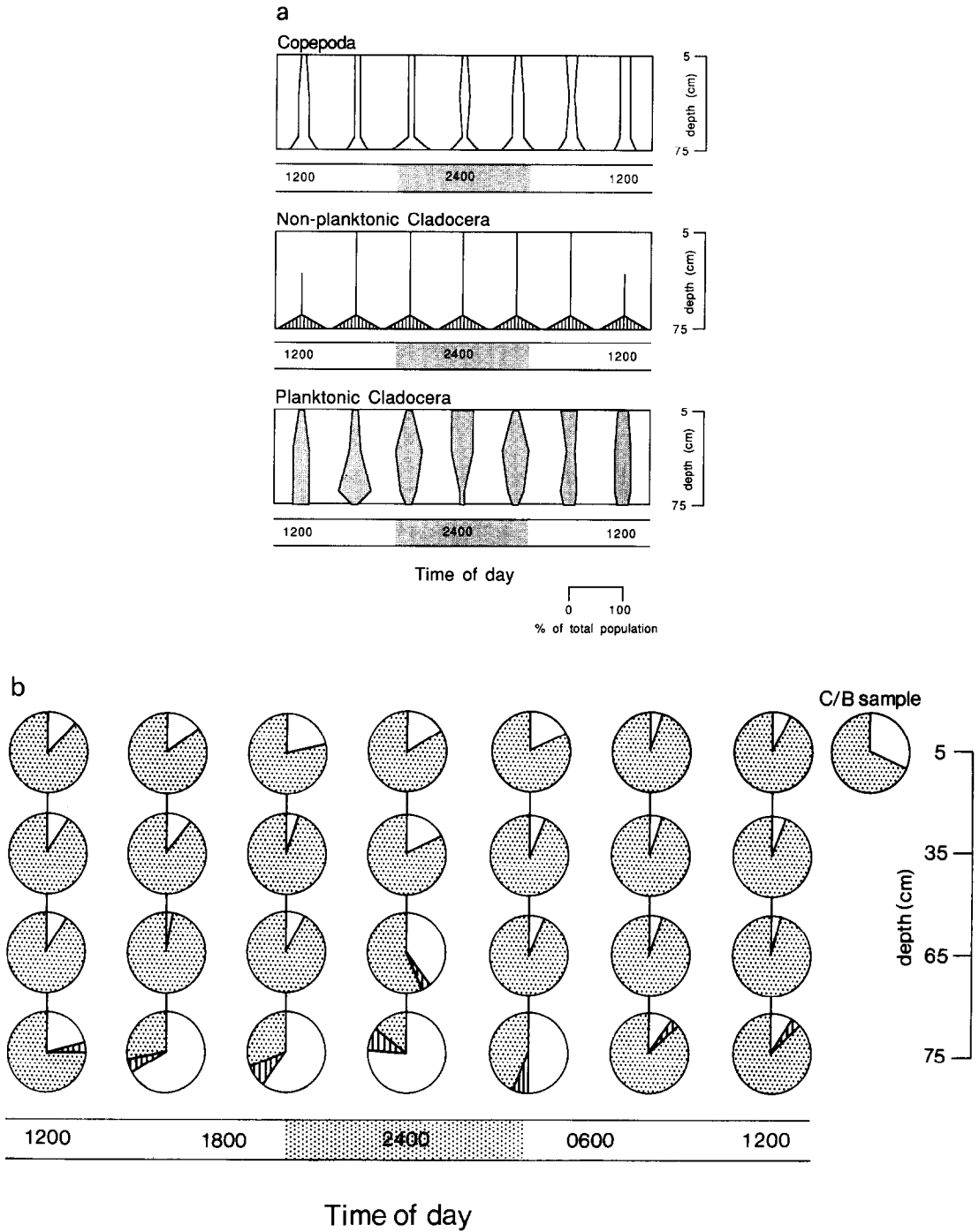1200 1800 2400 0600 1200

Time of day

Fig. 6. Spatio-temporal variations in the abundance and composition of the microcrustacean community. a – Kite diagrams showing the vertical distributions of Copepoda, non-planktonic Cladocera and planktonic Cladocera at 4 h intervals over a 24 h period; b – the resulting changes in composition of the microcrustacean community with depth and time. Composition according to Clarke-Bumpus sampling is also shown. Copepoda are represented by open segments, non-planktonic Cladocera by shaded segments and planktonic Cladocera by stippled segments. The shaded horizontal bars indicate the hours of darkness.

group in all samples except those taken from near the bottom of the lake during the hours of low light levels. Secondly, it is clear that the night-time microcrustacean community composition at the bottom of the water column differs fundamentally from that found near the surface during daytime (the Microcrustacea monitored by the Clarke-Bumpus sampler).

Discussion

Both bream and roach find copepods more difficult to capture than cladocerans, a finding also reported for a different assemblage of fish, copepods and cladocerans by Confer & Blades (1975). However, in the mixed prey trials the magnitude of this difference was much greater, with attack efficiencies on the copepods being significantly depressed when compared with those exhibited towards copepods presented alone. Detailed analysis of the fishes' attack behaviour indicated these differences in attack efficiency to be attributable to differences in the efficiency of their strikes. It has been shown elsewhere that fish may alter their strike tactics to improve their suction abilities (O'Brien 1979). Kettle and O'Brien (1978) reported that small lake charr (*Salvelinus namaycush*) attack copepods with a more vigorous strike (involving movement of the entire body) than that used against cladocerans, a pattern of behaviour which was also shown by several bream in the present study. The lower attack efficiencies on copepods when cladocerans were present may have been due to the fish making inappropriate 'cladoceran strikes' against the more elusive prey. Alternatively, the fish may have been electing not to waste energy making costly 'copepod strikes' when there were more easily captured prey available. Both of these behaviours will tend to lower the strike efficiency of the fish as it is defined here. The advantages to copepods to be gained by close association with preferred cladocerans in nature may be considerable (see Vinyard 1980). Another example of this multi-prey effect is reported by Persson (1985) who showed that when perch (*Perca fluviatilis*) are presented simultaneously with a cladoceran (*Daphnia magna*) and an

evasive macroinvertebrate (*Chaoborus obscuripus*), their attack efficiency on the latter is reduced in comparison with their performance on prey presented alone.

Both bream and roach consistently select cladocerans over copepods, even when the body size of the latter prey is considerably larger (our earlier laboratory work used prey of uniform size and hence had not addressed this topic). A similar selection pattern was recorded by Ivlev (1961) who observed bleak (*Alburnus alburnus*) to select a species of *Bosmina* over a relatively larger species of *Diaptomus* (a copepod of similar size to *Cyclops vicinus*). Additionally, Brooks (1968) reported that alewives (*Alosa pseudoharengus*) consumed *Daphnia catawba* before *Diaptomus minutus*, a pattern of selection which, as reasoned by Vinyard (1980), cannot be explained purely on the basis of size selectivity. From these reports and the results of our experiments we conclude that selection on the basis of escape ability is usually not overridden by selection on the basis of prey size.

The relative importance of copepods and cladocerans in the diets of bream and roach in May and June of 1982 were similar to those found in more extensive surveys reported in Winfield et al. (1983). Having shown that size selectivity cannot account for the discrepancy between predicted and observed bream diet, which contains a greater than expected proportion of copepods, we must turn to the alternative hypothesis that underyearling bream, perhaps in contrast to roach, feed mainly near the bottom of the lake during the hours of darkness when vertical migration by planktonic cladocerans has moved them out of this foraging location (for a review of vertical migration in Microcrustacea see Hutchinson 1976). This movement may make the prey community of the bottom of the lake at night radically different from that sampled by the Clarke-Bumpus sampler and used in our previous calculation of electivity indices.

This foraging location hypothesis is supported by the observation that the nocturnal bream, and to a lesser extent roach, spent the daylight hours in close proximity to a reedbed at the edge of the lake but at night ventured out into the open water. A similar horizontal diel migration was recorded for

these species by Bohl (1980) who suggested that this was a protective behaviour against optically orientated predatory fish and great crested grebes (*Podiceps cristatus* (L.)). Alderfen Broad possesses an abundant stock of piscivorous pike (*Esox lucius* (L.)) (Peirson 1986) and is also frequented by great crested grebes, common terns (*Sterna hirundo* (L.)) and black-headed gulls (*Larus ridibundus* (L.)) (I.J.W., personal observation), all of which may feed on bream and/or roach (Mann 1982, Cramp & Simmons 1977, Cramp 1985 and Cramp & Simmons 1983 respectively). The reedbed along the east shore of the lake provides the only dense structure in which young cyprinids can take refuge (at the time of these studies the lake was devoid of submerged macrophytes as a result of eutrophication (Moss 1983)). Such dense plant structure can interfere with the success of pike predation (Christiansen 1976, Peirson et al. 1985). The deeper distribution of the fish during the day than at night may also be an anti-predator adaptation since Kramer et al. (1983) consider that the surface layers of the water column will carry an increased risk of predation than greater depths when an aerial predator is present.

The assumption that the feeding depth of a fish can be determined from its vertical position of capture in a gillnet will not invariably be valid. For example, fish caught in the uppermost 20 cm of gillnets set in Alderfen Broad in March 1982 when zooplankton was scarce, contained non-planktonic cladocerans (*Chydorus* spp.) and sediment in their guts which they could only have obtained from the bottom of the water column (Winfield 1983). Similar gillnetting operations in deeper water by Berst & McCombie (1963) led them to also conclude that the vertical position of a fish in a gillnet may bear no relation to its feeding habits, a discrepancy which may arise from different catchabilities of foraging and non-foraging fish.

Our field investigations have led us to believe that bream and roach feed extensively under conditions of low light levels which contrast with those of our relatively brightly lit arenas. Although no work has been performed on roach, experiments with underyearling bream and another common European cyprinid, the minnow *Phoxinus phoxinus*

(L.), show that their foraging abilities on *Daphnia* are not appreciably impaired until light levels fall to at least below values associated with late dusk (Townsend & Risebrow 1982, Harden Jones 1956). We conclude that the behaviour of bream and roach feeding on cladocerans under natural conditions is similar to that observed in our arenas.

The situation with copepods is less straightforward due to the more complex nature of attacks on this prey type. The relationship between reaction distance, which is a function of light level (O'Brien 1979), and copepod escape ability was considered by Vinyard & O'Brien (1976) who pointed out that when a prey moves out of an attacking predator's reaction field it has in effect escaped, at least for the time being. It follows that when the reaction distance is small, the likelihood of fleeing behaviour by a copepod resulting in a successful escape will be increased (i.e. the predator chase efficiency will be decreased), although the ability of the prey to evade the strike itself may remain relatively unchanged. As our laboratory studies showed that the proportion of successful copepod captures involving a chase was smaller for bream than for roach, the net result of such changes in attack patterns is likely to improve the performance of bream relative to that of roach. Consequently, we consider that the use of our laboratory-derived attack efficiencies to predict relative patterns of prey selection and diet composition in the field remains a legitimate operation.

Group-specific diel vertical migrations were exhibited by the Microcrustacea of Alderfen Broad, despite the water column being only 75 cm deep, resulting in the community at the bottom of the lake at night becoming fundamentally different from that of the daytime surface. The effects of this difference on electivity indices for the June fish and prey data from the Clarke-Bumpus and selected pump samples of the 24 h exercise are shown in Table 4. Indices using the Clarke-Bumpus data are all similar to those found in our earlier extensive samples, with bream showing selection for copepods and against planktonic cladocerans and the opposite holding true for roach. For bream, these same trends are seen when they are assumed to have fed on the day and night surface prey compo-

Table 4. Electivity indices (mean ± 1 S.E.) of bream and roach from June 1982 for non-planktonic Cladocera (non-pl Clad), planktonic Cladocera (pl Clad) and Copepoda calculated using microcrustacean data from the Clarke-Bumpus sample and bottom and surface day and night pump samples. The index (Jacobs 1974) ranges from +1 to −1, positive values indicate positive selection while negative values indicate negative selection. A value of 0 is obtained when the predator shows no preference. The index is undefined when the prey type is absent from both the diet and the environment.

	Clarke-Bumpus	Bottom		Surface	
		day	night	day	night
Bream Copepoda	+0.988±0.003	+0.824±0.045	+0.001±0.166	+0.913±0.023	+0.867±0.034
non-pl Clad	undefined	−0.880±0.120	−0.932±0.068	undefined	−0.993±0.007
pl Clad	−0.988±0.003	−0.764±0.059	+0.304±0.172	−0.912±0.024	−0.865±0.034
Roach Copepoda	−1.000±0.000	−1.000±0.000	−1.000±0.000	−1.000±0.000	−1.000±0.000
non-pl Clad	undefined	−0.978±0.022	−0.990±0.010	undefined	−0.962±0.038
pl Clad	+0.934±0.066	+0.966±0.003	+0.999±0.001	+0.989±0.011	+0.993±0.007

sitions, and on the daytime bottom prey composition. However, calculations based on the nighttime bottom microcrustacean sample show a significant divergence from this pattern with a positive selection for the planktonic Cladocera, as predicted from laboratory results. In contrast, electivity indices calculated for roach are much less affected by available prey composition, reflecting the fact that roach feed extensively on open water zooplankton which shows little diel variation in composition. The ubiquitous negative selection for non-planktonic Cladocera shown by both fish may be the result of size selective predation within the cladoceran prey types with both fish avoiding the smaller benthic prey: other sampling has revealed that roach only feed extensively on non-planktonic cladocerans when planktonic Cladocera are scarce (Townsend et al. 1986).

Acknowledgements

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