

The effect of zooplankton abundance on feeding behaviour and prey size selection in Atlantic salmon, *Salmo salar*, alevins¹

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In an experiment on the effect of zooplankton density on feeding behaviour and prey size selection in Atlantic salmon (*Salmo salar*) alevins, total behavioural activity (feeding, social, ambiguous) was positively related to prey abundance up to a density of 350 items l⁻¹, after which activity peaked. Feeding error (missed attacks and/or rejected ingestions) increased with prey density. The likelihood that an alevin would attack an item upon which it had binocularly fixed (no. bites/no. visual fixes) peaked at densities of 270 items l⁻¹ and then declined. Feeding success (no. ingestions per bite or per fixation) also peaked and then declined. Changes in success were reflected in total number of items found in the gut. At high prey abundance (608 items l⁻¹) only 0.5–0.9 mm copepods were preferred components of alevin diets. Over all prey densities, preferred sizes of cladocerans and copepods did not overlap. These results may reflect a perceptual constraint (at high zooplankton densities) on alevin feeding behaviour.

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1. Introduction

Optimal foraging theory argues that predators should maximize their energy return per unit effort (Stephens and Krebs 1986). Foraging involves a cycle of behaviours interconnected with sensory modalities and skeletalmuscular systems. In such an interconnected multivariate system, every adaptive response becomes a factor in all subsequent adaptations. As a consequence, some traits may be at their selective optima while others are at their minima. There is no need to assume that all adaptive responses are ultimately or proximally optimal (see, e.g. Levins 1975). This is all the more true of juvenile fish predators which have incompletely developed sensory and skeletalmuscular systems, lack experience and lack learned predatory skills which themselves depend on an interconnected system of experience and anatomical development, a system rich in feedback (e.g. Blaxter 1970, Iwai 1980, Brown 1985, Marcotte and

Browman 1986, Balon 1986). Although most studies of optimal foraging in fish have considered only adult (or juvenile) behaviour and have assumed the predator's ability to correctly perceive a prey's size and thereby estimate its energetic value, a few studies have recognized that perceptual abilities and cognitive skills constrain universal optimality (e.g. Brown 1985, Ehlinger 1986, Marcotte and Browman 1986, O'Brien et al. 1986, Browman and Marcotte 1987, O'Brien et al. unpubl.).

Prey abundance is a fundamental variable in most studies dealing with a predator's choice of prey. As prey density increases, larval fish feeding rate, capture success, total ingestion, overall activity, gut evacuation time and growth rate all increase to an asymptote (or a peak) at some species-specific value (e.g. Wyatt 1972, Laurence 1974, Werner and Blaxter 1980, Houde and Schekter 1980, Theilacker and Dorsey 1981). There is some indication, however, that growth rate and gross

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growth efficiency decline from a peak reached at intermediate densities (see discussion below). The purpose of the experiments reported here was to detect the effects of zooplankton density on the feeding behaviour and prey size selection of Atlantic salmon alevins (sensu Balon 1975) in the context of the animals' perceptual abilities.

2. Methods

2.1. Aquarium set-up

Eleutheroembryonic Atlantic salmon, *Salmo salar*, were obtained from the North American Salmon Research Center in St. Andrews, New Brunswick, and the Florenceville Federal Fish Hatchery in Florenceville, New Brunswick, in May 1983. Experimental fish, of the same age (eight weeks after hatching) and size (25 ± 2 mm) were maintained under natural light in 91 l ($77 \times 32 \times 37$ cm) all-glass holding tanks. Aquaria were supplied with running freshwater from the hypolimnion of a nearby lake. The water was filtered through $64 \mu\text{m}$ mesh netting to prevent introduction of food and detritus, and was maintained at approximately 12°C (Browman and Marcotte 1986). Experimental and holding aquaria were surrounded on all sides with aqua green cloth to simulate the effects of light attenuation in freshwater (Lythgoe 1979), to prevent external movement from alarming the fish, and to dampen the effects of rapidly changing light intensity.

2.2. Feeding

Alevins were fed live zooplankton, twice daily (at a concentration of approximately 200 prey items l^{-1}), and had been feeding for 6–10 days prior to the experiments. Fish were starved for 18 hours prior to experimentation. Zooplankton was obtained each morning at the outflow of a small lake. The zooplankton assemblage gathered was similar to that encountered by alevins in the wild. The zooplankton obtained was mixed thoroughly and equal volumes were poured into beakers using the four-beaker sub-sampling method described by Van Guelpen et al. (1982). To introduce a given density of prey into experimental aquaria, standard volumes from these beakers were poured into the experimental tanks. Preliminary trials established that this method was accurate to within $\pm 15\%$. After each density trial the observation tank was emptied and thoroughly cleaned.

Air stones, placed in the center of each aquarium, created vortical water currents (which were laminar along the aquarium floor) upon which prey items were transported. The bubble curtain created by the airstone had no observable effect on alevin feeding behaviour. Pale green, 1 cm^2 graph paper was placed on the outer floor of each aquarium to enable estimation of the horizontal distance travelled by a particle in the current. In all experiments current speed in the areas where alevins fed was maintained at approximately $6\text{--}10 \text{ cm s}^{-1}$ (see

Rimmer and Power 1978) by regulating the air flow. Atlantic salmon alevins naturally orient their bodies into current (Rimmer and Power 1978, Wankowski 1981) so that this artificial situation at least partially simulated the normal feeding scenario. Fish were observed through rectangular viewports from behind a cardboard baffle. A shade was attached to the baffle and hung over the observer to minimize contrast effects and detection by the fish.

2.3. Behaviours observed

Alevins at this phase of development have relatively large and well-developed eyes, are visual predators (Protasov 1970, Wankowski 1981) and feed in an easily recognized sequence (Wankowski 1981, Browman and Marcotte 1986). The following sequential behaviours were enumerated using finger key counters: (1) eye fixation, (2) movement towards target, (3) bite, (4) miss, and (5) spit. Also enumerated were: (6) social interactions and (7) miscellaneous behaviours (non-feeding, non-social activity, e.g. yawn). All behaviours were observed under natural light between 1100 and 1400 hours to offset variability resulting from diurnal changes in behaviour (Browman and Marcotte 1986).

2.4. Treatments and replicates

Nine experiments were run, at different prey densities ($1\text{--}608$ items l^{-1}). Thirty naive fish were introduced into each observation tank. A minimum of 15 minutes was allowed for acclimation; preliminary observations had revealed that the behaviour of experimental fish became indistinguishable from those in the holding tank after 10 to 15 min.

Ten alevins, selected at random from the 30, were observed for a period of 3 min each. After 10 observation periods, 10 fish, selected at random were removed from the observation tank and immersed in concentrated formalin (preliminary trials revealed no regurgitation).

The guts of sacrificed fish were immediately injected with 10% formalin to arrest digestion. Whole fish were then preserved in 5% phosphate-buffered formalin. Guts were removed under a dissecting microscope and the number of cladocerans (with and without eggs), copepods, water mites, and miscellaneous other taxa present in the foregut was recorded. Incomplete prey items were counted only if the anterior section was present. All complete individuals were measured for length (copepods: prosome length; cladocerans: length without spine), to the nearest $100 \mu\text{m}$.

At the end of each trial, 1 l water samples were removed from the tanks by rapidly immersing a beaker into the feeding current. Zooplankton were preserved

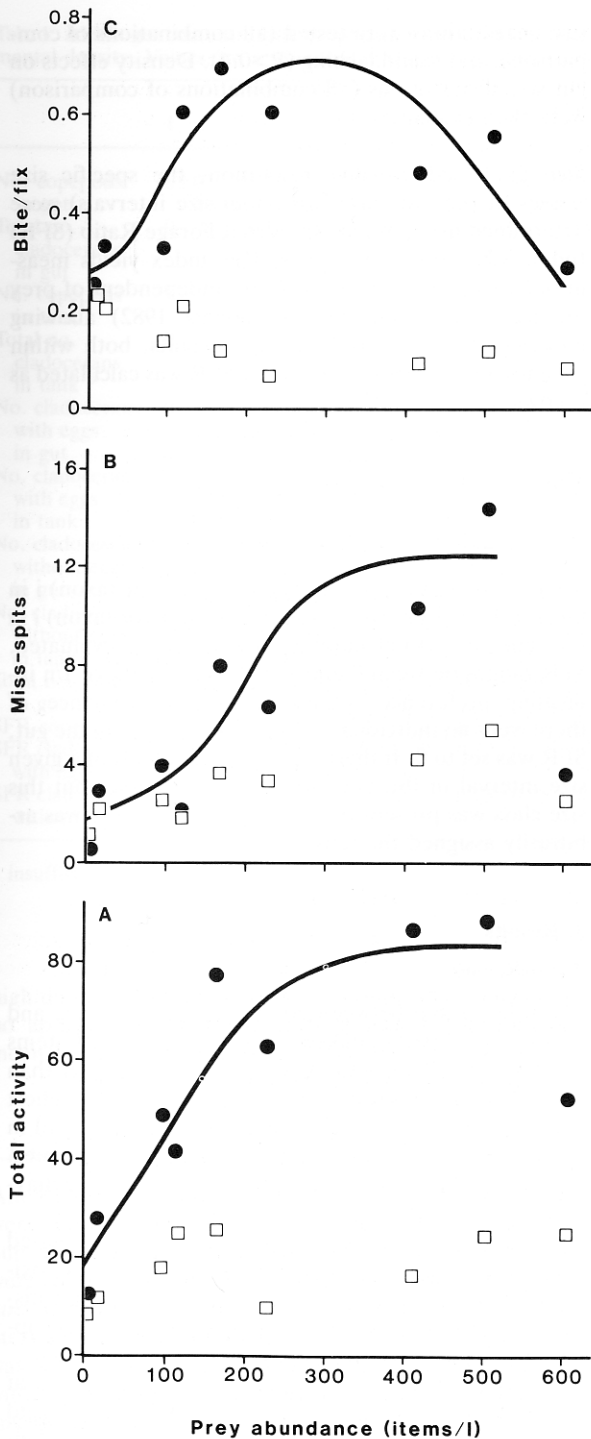


Fig. 1. The relationship between mean (for 10 fish) (A) total activity, (B) miss-spits, (C) bite/fix and tank zooplankton abundance. Squares are standard deviations around the means. Curves fitted by eye. The following density pairs were statistically discernable ($P < 0.05$) by multiple comparisons test: for (A) 1 vs 165, 226, 414, 510; 16 vs 165, 226, 414, 510; 117, vs 414, 510; 99 vs 414; for (B) 1 vs 165, 414, 510; 16 vs 414, 510; 99 vs 510; 117 vs 165, 414, 510; for (C) 1 vs 165, 226; 16 vs 165, 226; 99 vs 165, 226; 608 vs 165, 226, 510.

in 5% buffered formalin and subsequently examined for taxonomic composition. The number of individuals in different categories (as above) was recorded. The first 50 individuals of each group (or the total number present if less than 50) were measured for length (as above).

2.5. Behavioural data analysis

The behavioural data matrix was composed of 10 observations for each of the behaviours listed above, recorded for each of the nine density trials. As we were unable to replicate exact zooplankton densities, each trial was considered distinct in the analysis (for both behavioural and gut content analyses). Pairs of densities which were similar in value could have been used as replicates but this would not have changed the overall patterns observed. The following composite variables were calculated: (1) total activity: no. eye fixations + no. moves + no. bites + no. misses + no. spits + no. social + no. miscellaneous, (2) miss-spit (feeding error): no. of misses + no. of spits, (3) bite/fix: no. of bites/no. of fixes, (4) ingestion: no. of bites - (no. of misses + no. of spits), (5) success 1: no. of ingestions/no. of bites, (6) success 2: no. of ingestions/no. of fixes.

The nonparametric Kruskal-Wallis statistic (SAS - NPAR1WAY, option WILCOXON, Ray 1982) was employed to test the null hypothesis that density had no effect on a given composite variable. If the null hypothesis was rejected ($P < 0.05$), nonparametric Tukey-Type multiple comparisons (Daniel 1978) were calculated to establish the location(s) of any discernible difference(s).

2.6. Gut content analysis

2.6.1. Total number of items in the gut

The Kruskal-Wallis statistic was calculated (as above) to test the null hypothesis that density had no effect on the numbers of each taxonomic group present in the gut. If the null hypothesis was rejected ($P < 0.05$), multiple comparisons were calculated (as above).

Feeding selectivity on gross taxa (total numbers ingested) was evaluated using the Standardized Forage Ratio (SFR) Index (see below). The null hypothesis that density had no effect on index values was tested as above.

2.6.2. Prey size selection

Step 1: The Kolmogorov-Smirnov two sample test (Daniel 1978) was calculated to evaluate the size-frequency distributions of gut and tank items. Its null hypothesis is identity of two relative cumulative frequency distributions, one expected (tank) and the other observed (gut). As no between-fish differences in the size distributions of items in the gut were observed ($P > 0.40$), tests for differences between size-frequency distributions of gut and tank items were carried out on lumped data using the NPAR TESTS (option K-S) procedure of Statistical Package for the Social Sciences (SPSSX User's Guide 1983 edition). In the same way, density effects on tank

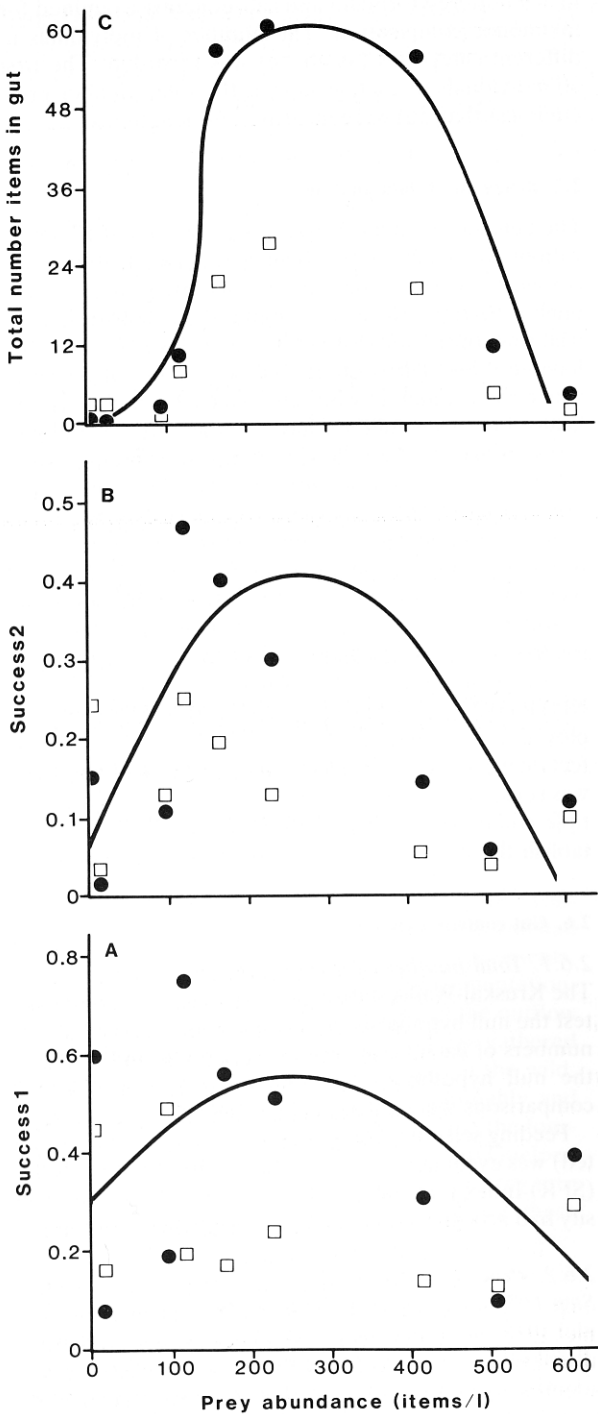


Fig. 2. The relationship between mean (for 10 fish) (A) success1, (B) success2, (C) number of items in alevin guts and tank zooplankton density. Squares are standard deviations around the means. Curves fitted by eye. The following density pairs were statistically discernible ($P < 0.05$) by multiple comparisons test: for (A) 16 vs 117, 165, 226; 510 vs 117, 165, 226; for (B) 1 vs 165, 226; 16 vs 117, 165, 226; 99 vs 165, 226; 510 vs 117, 165, 226; for (C) 1 vs 165, 226, 414, 510; 16 vs 165, 226, 414, 510; 99 vs 165, 226, 414; 608 vs 165, 226, 414.

size distributions were tested (all combinations of comparison), and found lacking ($P > 0.4$). Density effects on gut size distributions (all combinations of comparison) were then evaluated.

Step 2: To add further resolution, the specific size classes of prey preferred (0.2 mm size intervals) were determined using the Standardized Forage Ratio (SFR) Index (Chesson 1978, 1983). This index yields measurements of preference which are independent of prey or size class abundance (Lechowicz 1982) allowing meaningful comparisons of index results, both within samples and between treatments. SFR was calculated as follows:

$$\text{SFR}_i = \frac{r_i/p_i}{\sum_{i=1}^n r_i/p_i},$$

where r_i = proportion of prey size class (or taxon) i in the gut, P_i = proportion of prey size class (or taxon) i in the tank, n = total number of size classes evaluated. SFR ranges between 0 and 1, with values above $1/n$ indicating preference, values below $1/n$ avoidance. If there were no individuals of a given size class in the gut, SFR was set to 0. If there were no individuals of a given size interval in the tank zooplankton sample, but this size class was present in the gut, a value of 1% was arbitrarily assigned the tank interval.

3. Results

3.1. Behaviour

The relationship between zooplankton abundance and alevin total activity peaked at approximately 350 items l^{-1} (Fig. 1A). Peak activity was statistically higher than the low values associated with both the single highest and the low densities. There was no apparent trend in standard deviation around the mean activity values. This pattern was similar for all of the individual behaviours of which this variable is composed.

The parameter miss-spit (i.e. feeding error) increased with density, then dropped off suddenly at approximately 600 items l^{-1} (Fig. 1B). Low values were statistically discernible from peak values. There was no apparent trend in standard deviation around the mean.

The ratio bite/fix increased with density, peaked at 270 items l^{-1} , and then declined (Fig. 1C). Peak and lower values were statistically discernible. At low density, standard deviation appeared to be inversely related to the mean. The patterns for success 1 (Fig. 2A) and success 2 (Fig. 2B) were similar; an increase in success, peaking at 220–280 items l^{-1} for success 1 and 200–325 items l^{-1} for success 2, followed by a rapid decline as density increased further. Success at the intermediate densities was discernibly higher than at either low or

Tab. 1. Alevin gut contents, tank zooplankton composition and Standard Forage Ratio Index (SFR) summarized for each experimental density. Values are \pm standard deviations. SFR values > 0.33 indicate preference, < 0.33 avoidance.

	Density (no. l ⁻¹)								
	1	16	99	117	165	226	414	510	608
No. copepods in gut	0 \pm 0	0.2 \pm 0.6	1.9 \pm 1.5	8.1 \pm 7.7	30.5 \pm 8.5	41.7 \pm 23.0	19.5 \pm 11.6	9.4 \pm 5.0	3.8 \pm 3.8
Total no. cladocerans in gut	0	0.2	0.4	2.0	26.1	19.3	36.3	1.4	0.8
No. copepods in tank	1	1	22	58	59	60	186	94	106
Total no. cladocerans in tank	0	15	77	58	106	165	228	416	500
No. cladocerans with eggs in gut	0 \pm 0	0 \pm 0	0.3 \pm 0.48	0.8 \pm 1.2	13.3 \pm 7.3	9.4 \pm 4.1	21.4 \pm 8.2	0.5 \pm 0.85	0.5 \pm 0.71
No. cladocerans with eggs in tank	0	6	42	25	49	70	76	200	208
No. cladocerans without eggs in gut	0 \pm 0	0.2 \pm 0.6	0.1 \pm 0.32	1.2 \pm 1.0	12.8 \pm 10.2	9.9 \pm 4.7	14.9 \pm 7.3	0.9 \pm 1.1	0.3 \pm 0.48
No. cladocerans without eggs in tank	0	9	35	33	57	95	152	216	292
Total no. items in gut	0.3 \pm 0.5	0.4 \pm 0.8	2.3 \pm 1.6	10.5 \pm 8.4	56.6 \pm 21.9	61.1 \pm 28.3	56.0 \pm 20.1	10.8 \pm 5.5	4.6 \pm 4.2
SFR copepods	—*	—	0.89 \pm 0.14	0.62 \pm 0.25	0.54 \pm 0.14	0.69 \pm 0.17	0.23 \pm 0.15	0.93 \pm 0.08	0.82 \pm 0.34
SFR cladocerans with eggs	—	—	0.07 \pm 0.09	0.12 \pm 0.19	0.26 \pm 0.09	0.17 \pm 0.07	0.38 \pm 0.09	0.02 \pm 0.03	0.02 \pm 0.03
SFR cladocerans without eggs	—	—	0.05 \pm 0.14	0.25 \pm 0.25	0.20 \pm 0.11	0.14 \pm 0.10	0.19 \pm 0.07	0.05 \pm 0.09	0.08 \pm 0.15

* insufficient data for calculation

high densities. For both of these parameters, there was no apparent trend in standard deviation around the mean.

3.2. Gut contents

Almost all component taxa of the tank zooplankton were found in alevin guts. Some were present in low numbers and could not be evaluated statistically. These were: water mites (2 species), the cladocerans *Holopedium* sp. and *Alona affinis*, chironomid larvae, other dipteran larvae and oligochaetes. Thus, statistical analysis was limited to: (1) all calanoid and cyclopoid copepods, with no more than three species of either appearing at any time; and (2) cladocerans, primarily *Bosmina* sp., *Diaphanosoma* sp. and *Daphnia* sp. This composition of prey is similar to diets reported for Atlantic salmon alevins in the wild (e.g. White 1936, Williams 1981).

3.2.1. Total numbers of items in the gut

The number of prey items ingested was greatest over a density range of 180–350 items l⁻¹ and declined sharply on either side of this peak (Fig. 2C, Tab. 1). Peak values

were statistically discernible from the lower values associated with both low and high densities. Ingestion on either side of the peak was not statistically discernible.

There was strong selection for copepods, and against cladocerans (both with and without eggs), over all densities (Tab. 1). Density effects on SFR (for gross taxa) were not statistically discernible.

3.2.2. Prey size selection

Because of small sample sizes, size selection could only be evaluated for 6 of the 9 densities.

Step 1: Size frequency distributions of gut items were statistically discernible (K-S, $P < 0.005$) from those of tank items for all densities (Tab. 2); alevins were feeding selectively. The Mann-Whitney test revealed that the mean size of items in tank and gut were statistically different (M-W, $P < 0.001$; Tab. 2). Alevins preferred larger items, particularly copepods (Fig. 3).

Step 2: Alevin size selectivity for cladocerans and copepods is plotted in Fig. 3. At densities below 510 items l⁻¹ alevins preferred 0.5–0.9 mm cladocerans. At 510 items l⁻¹, the size range of cladocerans preferred narrowed to 0.6–0.8 mm, while at 608 items l⁻¹ cladocerans were not preferred. As density increased, the size

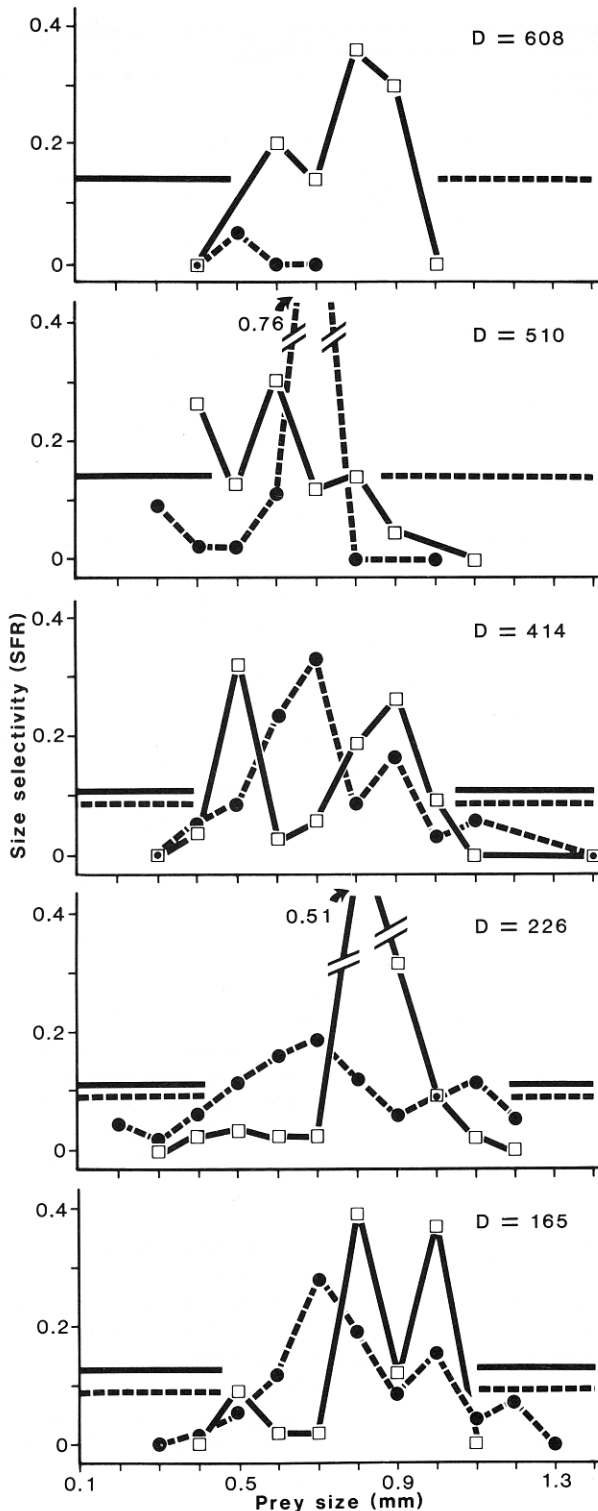


Fig. 3. The relationship between prey size selectivity (SFR) for copepods and cladocerans by prey density. D = zooplankton density (no. items/l). Solid line = copepods; Broken line = cladocerans. Values above the horizontal lines (solid for copepods, broken for cladocerans) represent preferred size classes, values below, those avoided.

range of copepods preferred decreased. There was little overlap in the sizes of cladocerans and copepods preferred.

4. Discussion

A number of recent studies have reported that abundant prey can confuse fish predators. This "confusion effect" results in an increase in the number of attacks per kill in prey groups of increasing size. The "confusion effect" apparently operates through the difficulty experienced by predators in singling out and tracking individual prey in a group (or at high density). Milinski (1977) found that three-spined sticklebacks preferentially prey on *Daphnia* which stray from swarms – the higher the swarm density, the higher the frequency of attacks on strays – and interpreted this as a behavioural reaction to overcome the "confusion effect". Milinski and Lowenstein (1980) reported that three-spined sticklebacks preferred prey which displayed "odd" swimming behaviour and Ohguchi (1981) reported that sticklebacks, when faced with high food densities, preferentially attack the most conspicuous prey (also interpreted as a means of limiting the "confusion effect"). Persson (1985) demonstrated that the foraging efficiency of fish (perch), feeding simultaneously on two prey species with different antipredatory behaviour, was reduced significantly. Recently, Landeau and Terborgh (1986) reported that largemouth bass, feeding on silvery minnows, quickly captured solitary prey but were less successful (and took much longer to make a capture) as prey school size increased. When minnows were artificially coloured, the bass overcame the "confusion effect" by attacking the conspicuous fish. O'Brien et al. (1986, unpubl.) and Evans (1986) have shown, for juvenile white crappie, that visual fields are reduced at high prey abundances (as are run speeds) and that overall search strategies may change in response to both the abundance and size of prey. It should be noted that these effects may be more pronounced in very young fish (see Milinski 1979, Marcotte and Browman 1986).

Indirect evidence for perceptual constraint/limitation in foraging larval fish has been reported. For example, Hunter and Thomas (1974) observed that anchovy larvae swam faster and fed more frequently in low density than in high density food patches. Munk and Kiorboe (1985) observed that the feeding rate of larval herring increased with density but reached an asymptote at approximately 100 copepod nauplii l^{-1} . They also observed that the water volume searched by herring larvae decreased as food density increased. It is possible that, in areas of low food density, the perceptual abilities of visually foraging larvae are not overwhelmed. As a result, their searching behaviour is not strongly limited (perceptually); they swim faster, make more frequent attempts at feeding, and are more successful.

In the present study, total alevin activity increased to a peak at approximately 350 items l^{-1} and then declined.

Tab. 2. Kolmogorov-Smirnov (Z) and Mann-Whitney (Z) results testing for differences in the size frequency distributions (K-S) and the mean lengths (M-W) of items in tank samples vs items in alevin guts. $P < 0.05$ indicates size selection. n = sample size.

Density	n gut	n tank	n total	K-S Z	P <	M-W Z	P <
117	72	107	179	2.41	0.0001	-3.63	0.0003
165	375	165	540	2.67	0.0001	-6.15	0.00001
226	381	225	606	2.46	0.0001	-6.78	0.00001
414	305	135	440	1.88	0.002	-5.31	0.00001
510	56	215	271	3.90	0.001	-5.71	0.00001
608	32	155	187	3.47	0.001	-3.33	0.0009

The animals reacted to increasing prey density by attempting to fix their eyes on the visual stimuli passing by them on the current. As prey abundance increased above 200 items l^{-1} , eye fixations on individual prey items became extremely rapid. Execution of subsequent feeding behaviours slowed, perhaps indicating a perceptual arrest in searching behaviour. That feeding error (miss-spit) increased with prey density is also evidence of alevin difficulty in reacting to high zooplankton concentrations (the sudden decline in miss-spit at 608 items l^{-1} appears to be anomalous, though we have no strong reason to discard it).

The ratio bite/fix is interpreted as the likelihood that alevins would attack an item upon which they had visually fixed. That this likelihood increased with prey density, peaked at 280 items l^{-1} , and then declined, also supports the conclusion that the perceptual abilities of the alevins became confounded at high prey densities. However, it may also indicate simply that, at high prey densities, there was not as much time available to bite as high a proportion of the items visually fixed. The parameters success 1 (ingestion/bites) and success 2 (ingestion/fixes) also support perceptual constraint. In both cases the number of ingestions (i.e. success) per unit effort (here a bite or a visual fix) increased with density to a peak and then declined. The number of items in the gut exhibited the same pattern: gut content peaked over a density range of 180 – 300 items l^{-1} and then declined. Thus, the effects of density on behaviour were reflected in gut content; above a threshold density, in this case approximately 300 items l^{-1} , alevins ingested fewer prey than at intermediate densities.

As already discussed, at intermediate and high prey densities, fish may minimize the “confusion effect” by concentrating their attention on rare or conspicuous items. Because large prey are usually scarcer than small prey, fish may continue to select large prey at intermediate densities, to avoid or reduce confusion (see Fig. 3). That alevin size preferences for cladocerans and copepods did not extensively overlap indicates that they may have been employing different strategies in prey capture or that they were “removing” size as a perceptually confounding variable. The exclusive preference for copepods at 608 items l^{-1} also indicates that alevins are concentrating on a single prey type in order to reduce confusion at high prey abundance; it could be ar-

gued that copepods, because of their intermittent swimming behaviour, are more conspicuous (against a background of continuously-swimming cladocerans) at high prey densities (see Milinski and Lowenstein 1980, Ohguchi 1981). In addition, many of the cladocerans consumed, including very small ones, carried eggs (Tab. 2) perhaps indicating that, because of the opaque egg mass, they were more visible (see Mellors 1975, Winfield and Townsend 1983). In the gut, small cladocerans were found lying next to large copepods suggesting that at least some small prey items were ingested incidentally, not an uncommon occurrence in planktivorous fish (Wright and O'Brien, pers. comm.).

The effect of high prey abundance on salmon alevins in the wild is unclear. During most of the summer, the abundance of invertebrate drift in rivers and streams rarely exceeds 100 items l^{-1} (Hynes 1970, Allan 1983). During the spring, however, zooplankton and zoobenthos densities in lakes and streams can be much higher (e.g. short duration pulses of 200 – 800 items l^{-1}). As this is the time when salmon hatch and exit the gravel, the effects of high prey abundance on alevin behaviour reported here could be of both proximate and ecological/evolutionary significance.

Christensen et al. (1980), in an attempt to model size selective predation in larval fish, have employed, at least in part, optimal foraging theory to explain patterns of prey size selection by fish; increasing food abundance should lead to greater food specialization. Our results indicate that the range of prey sizes ingested by salmon alevins decreased with increasing prey density and that the preferred size classes of copepods and cladocerans did not overlap (Fig. 3). It is noteworthy that both optimal foraging theory and perceptually based hypotheses can lead to this same prediction (also, see Marcotte and Browman 1986, O'Brien et al. unpubl.).

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