

Diurnal feeding and prey size selection in Atlantic salmon, *Salmo salar*, alevins*

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Synopsis

Results of an experiment on diurnal feeding behaviour and prey size selection in Atlantic salmon, *Salmo salar*, alevins are reported. Peaks in total behavioural activity, ingestion rate, feeding success (# of ingestions per unit effort) and feeding error (total number of prey missed or rejected after an attack) occurred in the early morning (0600–0900 h), at mid-day (1100–1400 h) and in the evening (1900–2000 h). Variability in feeding success decreased as its mean value increased and variability in feeding error decreased as error decreased. This pattern in the behavioural indices which reflect the alevin's ability to execute spatially-oriented activities (i.e. prey size selection, success, error) is put forward as a possible manifestation of underlying rhythms in the animal's nervous system. In the early morning alevins fed selectively on the largest copepods (>0.8 mm). This restricted range of selectivity was associated with low light levels and high activity. Later in the day, a broader range of the larger size classes were selected (>0.7 mm). Intensity of selection was inversely associated with total activity. This evidence of diurnal pattern in alevin feeding behaviour shows that (1) fish exhibit behavioural rhythms early in their life history, and (2) prey size selection, in terms of both intensity and breadth of size class selected for, changes over the day.

Introduction

Rhythms in fish physiological functions, locomotor activity, schooling and feeding behaviour have been widely reported in the literature (e.g. Schwassmann 1971, Thorpe 1978). In general, fish are most active at dawn and dusk, though the timing of rhythms varies among fish species and habitat and is at least partially dependent upon a host of environmental variables (Manteifel et al. 1978, Schwassmann 1979).

Despite a growing body of information, endo-

genous and/or exogenous rhythms in fish feeding behaviour have been largely overlooked in studies not directly concerned with them. As a result, rhythms have not generally been controlled for in studies of fish feeding nor have their effects on patterns of size selection been closely examined.

Rhythms in larval fish behaviour, though not unknown (e.g. Oliphant 1957, Blaxter 1965, Godin 1981), have received far less attention, partly because the small size and fragility of larval fish limits their suitability for feeding experiments. Prey size selection in larval fish is also known (e.g. Beyer et

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al. 1980, Christensen et al. 1980, Checkley 1982, Mikheev 1984) but has not generally been examined in conjunction with, or in relation to, rhythms in feeding behaviour.

We report the results of an experimental study on Atlantic salmon alevins (*sensu* Balon 1984) with goals of (1) quantitatively describing diurnal patterns (rhythms) in activity, feeding behaviour and prey size selection; (2) establishing a connection among these patterns; and (3) discussing the significance of these results, and rhythms in general, to the study of fish feeding.

Materials and methods

Unfed alevins of Atlantic salmon, *Salmo salar* L., 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 approximately the same age and size (25 mm), were maintained under natural lighting conditions in identical holding tanks (77 L \times 32 D \times 37 cm H: 91 liters) at the Huntsman Marine Laboratory, St. Andrews, New Brunswick. All experiments were conducted under natural light. Aquaria were supplied with running freshwater from the hypolimnion of a nearby lake. The water supply was filtered through 64 μ m mesh to prevent introduction of unwanted material and was maintained at approximately 12°C (Lemm & Hendrix 1981). A natural assemblage of live zooplankton was added to holding tanks twice daily at a concentration of approximately 200 items per liter. Alevins had been feeding for 4 days prior to the experiment. Feeding of fish was discontinued 8 h prior to experimentation by removing them to a holding tank containing only filtered water.

Experimental and holding aquaria were surrounded with aqua-green cloth to simulate light attenuation in fresh water (Lythgoe 1979, Gibson 1980), prevent external movement from alarming the fish, and dampen the effects of rapidly changing light intensity. Pale green, 1 cm² graph paper was placed on the outer floor of each aquarium to aid in the estimation of horizontal distances. Air stones

placed in the center of each aquarium created vertical 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. Current speed in the areas where fish fed was maintained at approximately 6–10 cm \cdot sec⁻¹ (see Rimmer & Power 1978) by regulating the air flow. Estimates of current speed were obtained by measuring the distance, per unit time, travelled by a particle in the feeding current. Atlantic salmon alevins naturally orient into current (Kalleberg 1958, Rimmer & Power 1978, Wankowski & Thorpe 1979) so that this artificial situation provided a reasonable simulation of natural feeding conditions.

Alevins are approximately 25 mm long at this interval of development, have relatively large and well-developed eyes, are visual predators (Protasov 1970, Wankowski 1981) and feed in an easily recognized sequence (e.g. Mills 1971, Mighell 1981, Wankowski 1981). The following sequential behaviours were enumerated using finger key counters:

Eye fixation = biocular locking of an alevin's eyes on a target.

Movement towards target = motion of the entire body, or head region only, towards the item visually targeted.

Bite = opening-snapping-closing of the jaws on the item.

Miss = unsuccessful bite.

Spit = forceful rejection of an item from the buccal cavity.

Also enumerated were: *Social behaviours* = interactions with other alevins.

Ambiguous behaviours = non-feeding, non-social activity (e.g. yawn).

Alevins, oriented into the current, lay on the substrate using pectoral fins for support and stabilization. When a target carried by the current passed by, the fish either exhibited the feeding behaviour sequence or ignored it. 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.

To examine diurnal changes in feeding behaviour alevins were observed on an hourly basis between 0600 h and 2100 h, the hours during which enough light was available for reliable observation. Light intensity (lux) at the water surface was recorded hourly using a Gossen Lunasix 3 light meter.

At 0500 h, 30 naive alevins were removed from a holding tank and were placed in an observation tank. The following procedure was repeated hourly for the duration of the experiment. Ten alevins, selected at random from the 30, were observed for a period of 3 min each. After 10 observation periods, 10 alevins were removed from the observation tank and sacrificed by immersion in concentrated formalin (preliminary trials revealed no regurgitation). Ten unfed and naive alevins were added to the observation tank to replace those removed. A minimum of 15 min was allowed for acclimation (preliminary observations had revealed that the behaviour of added fish became indistinguishable from those already present after 10 to 15 min).

The fish were fed on zooplankton obtained each morning at the outflow of Wheaton Lake, New Brunswick, a small, eutrophic, pristine glacial lake. A plankton net (125 μm mesh) was placed in the lake outflow for 15 min. The contents were transferred into clean buckets, transported to the laboratory, and filtered through a 1 mm mesh to remove large organisms and extraneous material. To introduce a standard amount of food into the experimental aquarium, the filtrate was mixed thoroughly and equal volumes were poured into beakers using the four-beaker sub-sampling method (Van Guelpen et al. 1982). Known volumes from these beakers were poured into the tanks at the outset of the experiment and, to replenish prey numbers depleted by feeding, at 60 min intervals over its course. Preliminary trials established that this method was accurate to within $\pm 15\%$ (Table 3).

The guts of sacrificed fish were immediately injected with 10% formalin to arrest digestion. Whole fish were then preserved in 5% phosphate-buffered formalin (Markle 1984). Fork length, body width immediately behind the pectoral fins,

and mouth width were recorded to the nearest millimeter. Guts were removed under a dissecting microscope. The numerical composition of gross taxonomic groups (cladocerans with and without eggs, copepods, water mites, miscellaneous) present in the foregut was recorded. Incomplete prey items were counted only if the anterior section was present. All well-preserved individuals were measured for length (copepods: prosome length; cladocerans: length without spine) using an ocular micrometer.

At the end of each hour, 11 water samples were removed from the tanks by rapidly immersing a beaker into the feeding current. Tank zooplankton samples were preserved in 5% buffered formalin and subsequently examined for taxonomic composition. The numerical composition of gross taxonomic groups (as above) was recorded by examination of the entire sample under a dissecting microscope. The first 50 individuals (or the total number present if less than 50) of each group were measured for length (as above).

Data analysis

Behaviour data. – The behavioural data matrix was composed of 10 observations for each of the behaviours listed above, recorded hourly over the 15 h of the experiment. As prey density varied somewhat between hours (Table 3) the behavioural variables were normalized by dividing the number of observations of each behaviour by the total number of prey items available in a given time period. Because the effect of density on these feeding parameters is linear at low values (Browman & Marcotte, unpublished), normalization should not have introduced bias.

The following composite variables were calculated from normalized data:

Total activity: = # eye fixations + # moves + # bites + # misses + # spits + # social + # ambiguous,

Miss-spit (feeding error): # of misses + # of spits,

Bite/fix: # of bites/# of fixes,

Ingestion: # of bites – (# of misses + # of spits),

Success 1: # of ingestions/# of bites,
 Success 2: # of ingestions/# of fixes.

All variables were tested for normality using a one sample Kolmogorov-Smirnov test (UNIVARIATE procedure of the Statistical Analysis System, SAS User's Guide, 1982 edition). Because there was significant deviation from normality, the nonparametric Kruskal-Wallis statistic (Daniel 1978; SAS – NPAR1WAY, option WILCOXON) was employed to test the null hypothesis that time of day had no effect on a given composite variable. If the null hypothesis was rejected ($P < 0.05$), nonparametric Tukey-Type multiple comparisons (Zar 1984) were calculated to establish the location(s) of any discernable difference(s).

Gut content data

Total number of items in the gut. – The number of individuals of each taxonomic group present in the gut were normalized by dividing each by the numbers of individuals of the corresponding group present in the tank. The Kruskal-Wallis statistic was calculated (as above) to test the null hypothesis that there were no diurnal differences in normalized 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, not normalized) was evaluated using the Standardized Forage Ratio (SFR) index (see below). The null hypothesis that there were no diurnal differences in these indices was tested as above.

Prey size selection. – Our goal here was to determine whether alevis selected among prey sizes nonrandomly and, if this was the case, to evaluate the intensity of size selection and determine which size classes were preferred. Towards this end, the following three-step approach was used.

Step 1. The Kolmogorov-Smirnov two sample test (Hollander & Wolfe 1983) 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, hourly changes in tank size distributions were tested (all combinations of comparison), and found lacking ($P > 0.4$). Diurnal differences in gut size distributions (all combinations of comparison) were then evaluated.

Step 2. Once selection was established, its intensity was evaluated using Bartell's (1982) Index of Selection Intensity

$$S = \frac{L_I - L_T}{L_R},$$

where L_I = mean length of ingested prey, L_T = mean length of prey in tank, L_R = range of prey lengths over gut and tank samples, and S = selection intensity.

S ranges from -1 to $+1$; values near zero indicate no size selection; high positive values indicate intense selection for large prey; high negative values intense selection for small prey. Lengths beyond ± 2 standard deviations of mean values were omitted as they affect the index nonlinearly (Bartell 1982).

The null hypothesis that there were no diurnal differences in intensity of size selection was tested using the nonparametric one sample Wilcoxon signed ranks test (Hollander & Wolfe 1983). A discernable difference ($P < 0.05$) for any given test leads to the conclusion that the particular S -value tested (i.e. the intensity of selection at that hour) is different from all of the other S -values (i.e. the intensity of selection at all other hours). The tests were carried out using Statistics Plus (option WILCOXON SIGNED RANKS TEST), a general statistics package for the Apple II computer (Madigan & Lawrence 1982).

In addition to testing for diurnal differences in S , the degree of association (correlation) between time of day and intensity of size selection was evaluated. The nonparametric Spearman rank correlation coefficient (RHO) was calculated because (1)

it could not be assumed that diurnal effects on selection intensity were linear, (2) the data were not bivariate normally distributed (tested as above) and (3) as a result of (1) and (2) the standard product-moment correlation coefficient (r) was not applicable (Daniel 1978). RHO varies between -1 and $+1$, with a value of $+1$ indicating perfect direct relationship between variables, and a value of -1 indicating perfect inverse relationship. The test was carried out using Statistics Plus (option Spearman RHO).

Step 3. 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). The index yields measurements of preference which are independent of prey or size class abundance (Lechowicz 1982, Pearre 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, and 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 0.1% was arbitrarily assigned the tank interval.

Results

Behaviour

Total activity (Fig. 1) was highest in the early morning, followed by less pronounced mid and late day rises. Variance (in the form of standard deviation) was positively related to the mean. This pattern

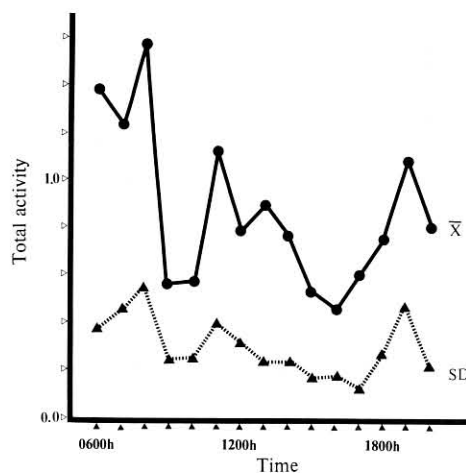


Fig. 1. The relationship between mean (for 10 fish) Total activity (# eye fixations + # moves + # bites + # misses + # spits + # social + # ambiguous) per 3 min observation period (normalized for tank zooplankton abundance) and time of day. SD = standard deviation (broken line) around the mean (solid line). The following hour pairs were statistically discernable, by multiple comparisons test, at the level of probability (P) indicated: 0600 and 0800 h vs 0900, 1000, 1500, 1600, 1700 h ($P < 0.01$); 0700 h vs 0900, 1000, 1500, 1600 h ($P < 0.06$); 0900 h vs 1100 h ($P < 0.08$); 1100 h vs 1500, 1600 h ($P < 0.05$); 1600 h vs 1900 h ($P < 0.06$).

was similar for all of the singular behaviours of which this composite variable, and those which follow, were composed. Miss-spit (i.e. feeding error) followed the same general trend, though the late-day trough and peak were not statistically discernable (Fig. 2). Bite/fix (Fig. 3) exhibited an extended early morning peak followed by a sharp depression, then a gradual rise. The late day peak was not statistically discernable. Variance in Bite/fix was inversely related to the mean.

For Ingestion (Fig. 4) and Success 1 (Fig. 5) only early morning peaks were statistically discernable. The 1000 h peak in Success 1 was associated with an anomalously low number of Bites in that time period. The variance of Success 1 was positively related to its mean. Variance in Ingestion exhibited a 3 peak rhythm while its mean decreased monotonically. The early morning peak-trough of Success 2 was statistically discernable from values later in the day (Fig. 6). Mean values over the remainder of the day followed a pattern inverse of the trends in the other behavioural variables. Variance in Suc-

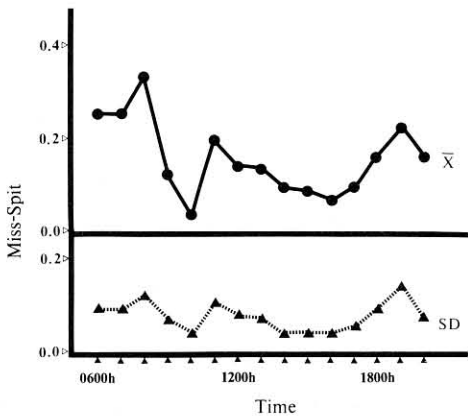


Fig. 2. The relationship between mean (for 10 fish) number of miss-spits (# misses + # spits, i.e. feeding error) per 3 minute observation period (normalized for tank zooplankton abundance) and time of day. SD = standard deviation (broken line) around the mean (solid line). The following hour pairs were statistically discernable, by multiple comparisons test, at the level of probability (P) indicated: 0600 and 0700 h vs 1000, 1500, 1600 h ($P < 0.05$); 0800 h vs 0900, 1000, 1400, 1500, 1600, 1700 h ($P < 0.05$); 1000 h vs 1100, 1800, 1900, 2000 h ($P < 0.06$).

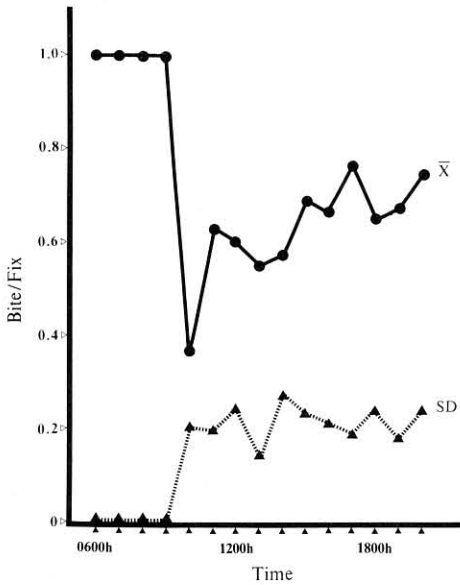


Fig. 3. The relationship between mean (for 10 fish) number of bite/fixes (# bites/# fixes) per 3 minute observation period (normalized for tank zooplankton abundance). The following hour pairs were statistically discernable, by multiple comparisons test, at the level of probability (P) indicated: 0600 h vs 1000, 1100, 1200, 1300, 1400 h ($P < 0.05$); 0700 h vs 1600, 1800, 1900 h ($P < 0.08$).

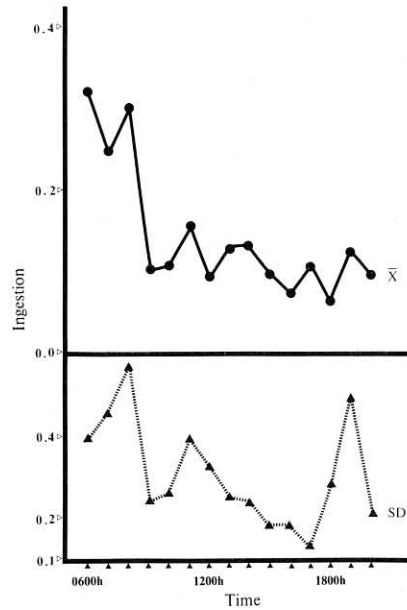


Fig. 4. The relationship between mean (for 10 fish) number of Ingestions (# Bites - # Miss - # Spits) per 3 minute observation period (normalized for tank zooplankton abundance) and time of day. SD = standard deviation (broken line) around the mean (solid line). The following hour pairs were statistically discernable, by multiple comparisons test, at the level of probability (P) indicated: 0600 h vs 1000, 1200, 1500, 1600, 1800, 2000 h ($P < 0.05$); 0700 h vs 1600, 1800 h ($P < 0.05$); 0800 h vs 1600, 1800 h ($P < 0.05$).

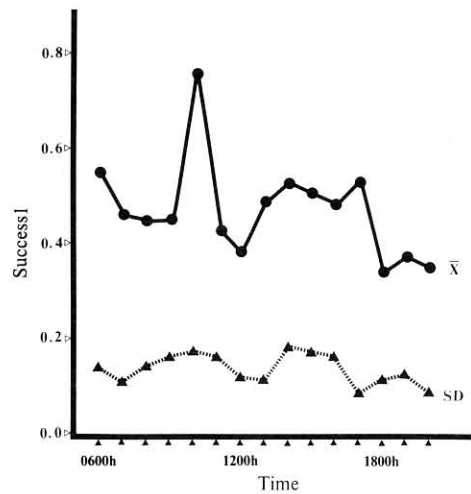


Fig. 5. The relationship between mean (for 10 fish) feeding success (# ingestions/# bites, i.e. Success I) per 3 min observation period (normalized for tank zooplankton abundance) and time of day. SD = standard deviation (broken line) around the mean (solid line). The following hour pairs were statistically discernable, by multiple comparisons test, at the level of probability (P) indicated: 1000 h vs 1200, 1800, 1900, 2000 h ($P < 0.05$).

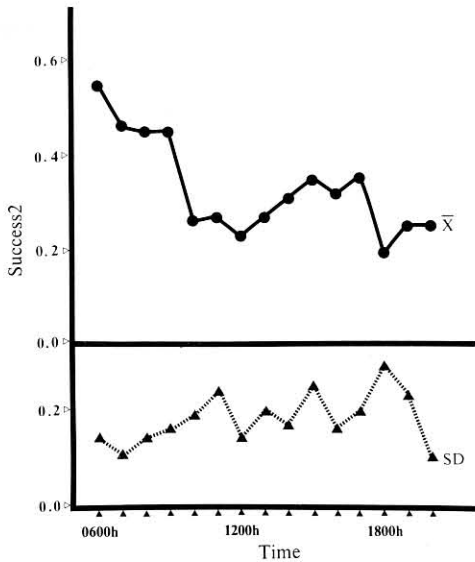


Fig. 6. The relationship between mean (for 10 fish) feeding success (# ingestions/# fixes, i.e. Success 2) per 3 minute observation period (normalized for tank zooplankton abundance) and time of day. SD = standard deviation (broken line) around the mean (solid line). The following hour pairs were statistically discernable, by multiple comparisons test, at the level of probability (P) indicated: 0600 h vs 1000, 1100, 1200, 1800, 1900, 2000 h ($P < 0.05$); 0600 h vs 1300 h ($P < 0.06$); 0700 h vs 1200, 1800 h ($P < 0.06$); 0800 h vs 1800 h ($P < 0.05$); 0900 h vs 1800 h ($P < 0.05$).

cess 2 was inversely related to its mean.

In general, the most pronounced peaks occurred in the early morning (0600–0800 h), followed by a morning trough (0900–1000 h), a mid-day rise (1100–1400 h), another trough (1500–1800 h) and a late day rise (1900–2000 h). This trend in the mean values of each composite variable was consistent, although the entire trend was not statistically discernable in all cases.

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 fly 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 (White 1936, Allen 1941, Pinski 1967, Arnemo et al. 1980, Williams 1981).

Total number of items in the gut

In general, there were no discernable diurnal differences in the total number of items present in the gut (Table 1); the number of copepods in the gut was discernably different for 0600 versus 0800 h ($P < 0.05$). High variance in the numbers may have been responsible for this lack of resolution (e.g. a single fish could contain anywhere from 0 to 60 items).

There was strong selection for copepods, and avoidance of cladocerans, over all hours. Diurnal changes in selection were not statistically discernable, though variability in selection, as reflected in the standard deviation of the indices, was greater in the early morning (Table 1).

Prey size selection

Step 1 (presence of size selection): Sample sizes were sufficient to evaluate size selection for 8 of the 15 h of observations (Table 2). Sizes of items in the gut were generally greater than those in the tank. With the exception of 0600 h, all size distributions of items in the guts were statistically discernable from the size distributions of items in the tank, indicating that alevins were feeding selectively (Feller & Kaczynski 1975); sizes of items in the gut were greater than those in the tank. The distribution of sizes selected, compared among fish over different hours, was significantly different for 0600 versus 1700 h (K-S $Z = -0.490$, $P < 0.05$), 0600 versus 1800 h (K-S $Z = +0.595$, $P < 0.02$), and 1000 versus 1800 h (K-S $Z = -0.420$, $P < 0.05$) indicating that, for these hour pairs, there were differences in size selection.

Step 2 (intensity of size selection): Selection intensity (Bartell's S) was significantly lower in the early morning and at mid-day (Fig. 7), with significantly higher selection intensities occurring in the

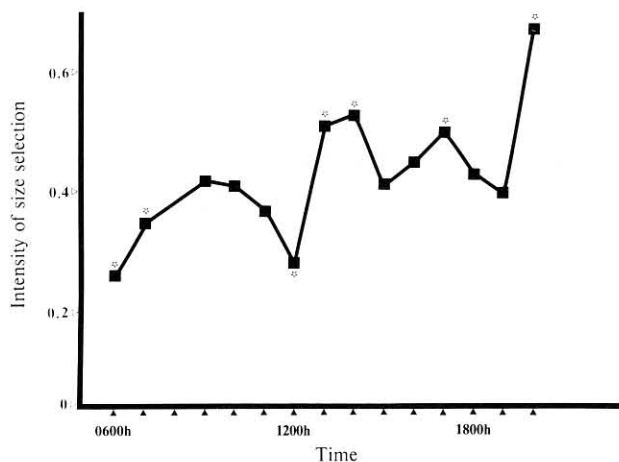


Fig. 7. The relationship between intensity of size selection (Bartlett's S) and time of day. Stars (*) associated with points indicate that the S value for that hour is statistically different ($P < 0.05$) from all other hours.

Discussion

Until recently, studies of feeding in larval fish had been limited to qualitative reports of feeding behaviour and/or gut contents. Contemporary inves-

tigations have begun to examine more closely the relationships between the feeding and biology of young fish and environmental variables with their inherent periodicities (Blaxter 1965, Rosenthal 1969, Houde & Shekter 1980, Hunter 1980, Godin 1981, Williams 1981, Balon 1986). The quantitative evidence of diurnal pattern in alevin feeding behaviour reported here shows that: (1) fish exhibit behavioural rhythms early in their life history; (2) their daily feeding behaviour is complex and variable; and (3) prey size selection, in terms of both intensity and breadth of size class selected for, begins soon after first exogenous feeding and changes over the day.

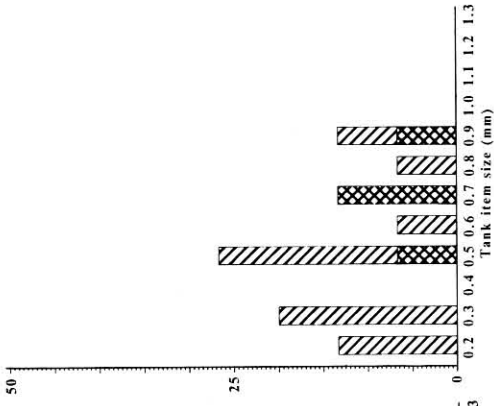
The observed pattern in total alevin activity was similar to that reported in the literature for Atlantic salmon. In a qualitative study, Pinskii (1961, 1962) observed two periods of intensified feeding activity, one in the early morning and another in the late day; the former was 1–1.5 times greater than the latter. As Atlantic salmon alevins do not feed at night (Hoar 1942, Pinskii 1961, 1967, personal observation), the early morning peak was not surprising. Under the conditions of our experiment, al-

Table 3. Hourly summaries of (1) Bartlett's index of selection intensity (S), (2) the probability (P) that any given value of S is different from all others, (3) light intensity and (4) tank zooplankton density.

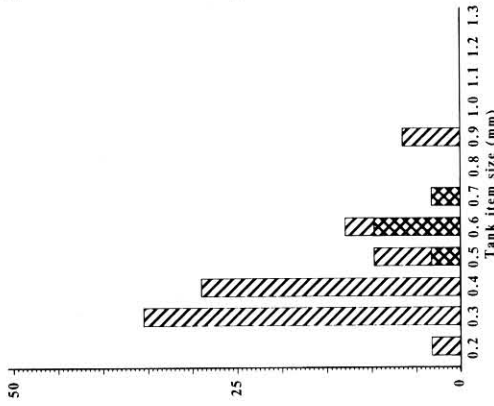
Hour	S	P <	Light intensity (lux)	Tank zooplankton density (number per liter)
0600	0.26	0.001	1.75	27
0700	0.35	0.024	66	23
0800*	–	–	175	27
0900	0.42	0.65	260	30
1000	0.41	0.59	700	31
1100	0.37	0.052	1200	31
1200	0.28	0.002	1500	30
1300	0.51	0.018	700	33
1400	0.53	0.011	1200	30
1500	0.41	0.59	1600	47
1600	0.45	0.47	480	41
1700	0.50	0.67	300	46
1800	0.43	0.60	500	39
1900	0.40	0.60	140	34
2000	0.67	0.001	66	38
			mean =	33.8
			S.D. =	7.0

* Insufficient data for calculation of S.

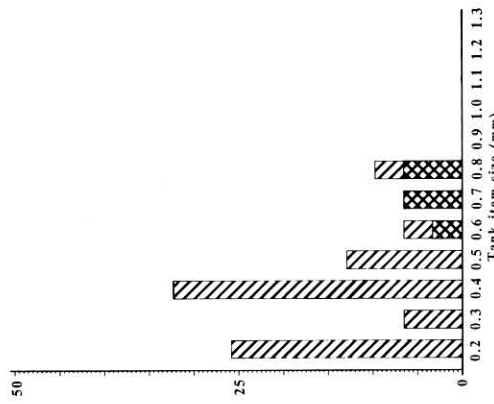
Hour of trial = 12



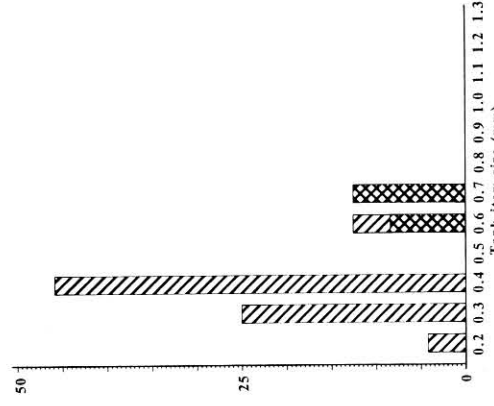
Hour of trial = 11



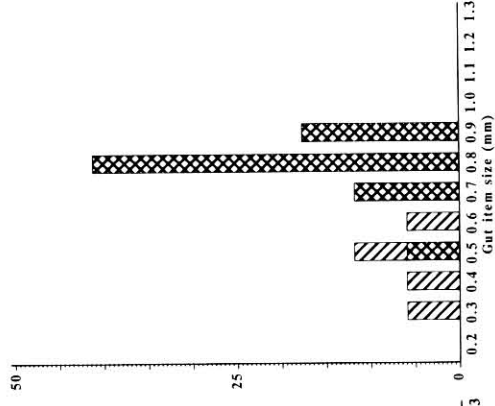
Hour of trial = 10



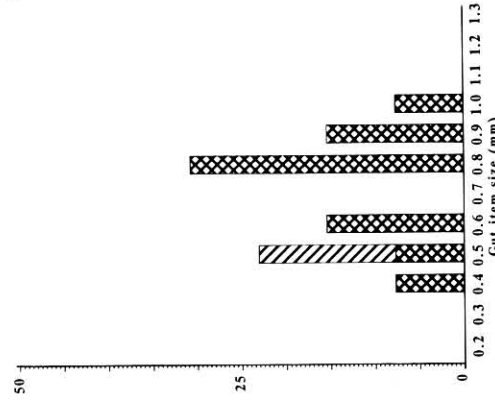
Hour of trial = 6



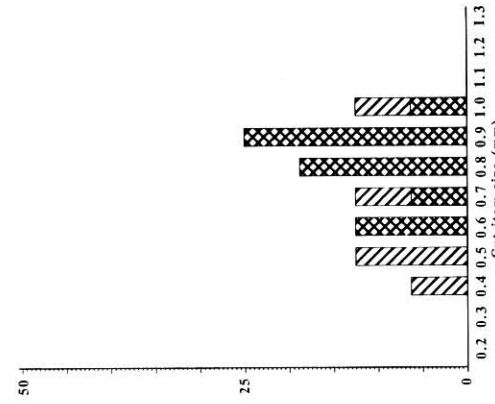
Hour of trial = 12



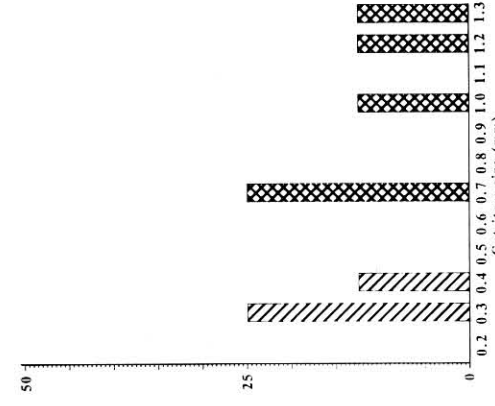
Hour of trial = 11



Hour of trial = 10



Hour of trial = 6



Taxon Copepods Cladocerans

Taxon Copepods Cladocerans

Taxon Copepods Cladocerans

Taxon Copepods Cladocerans

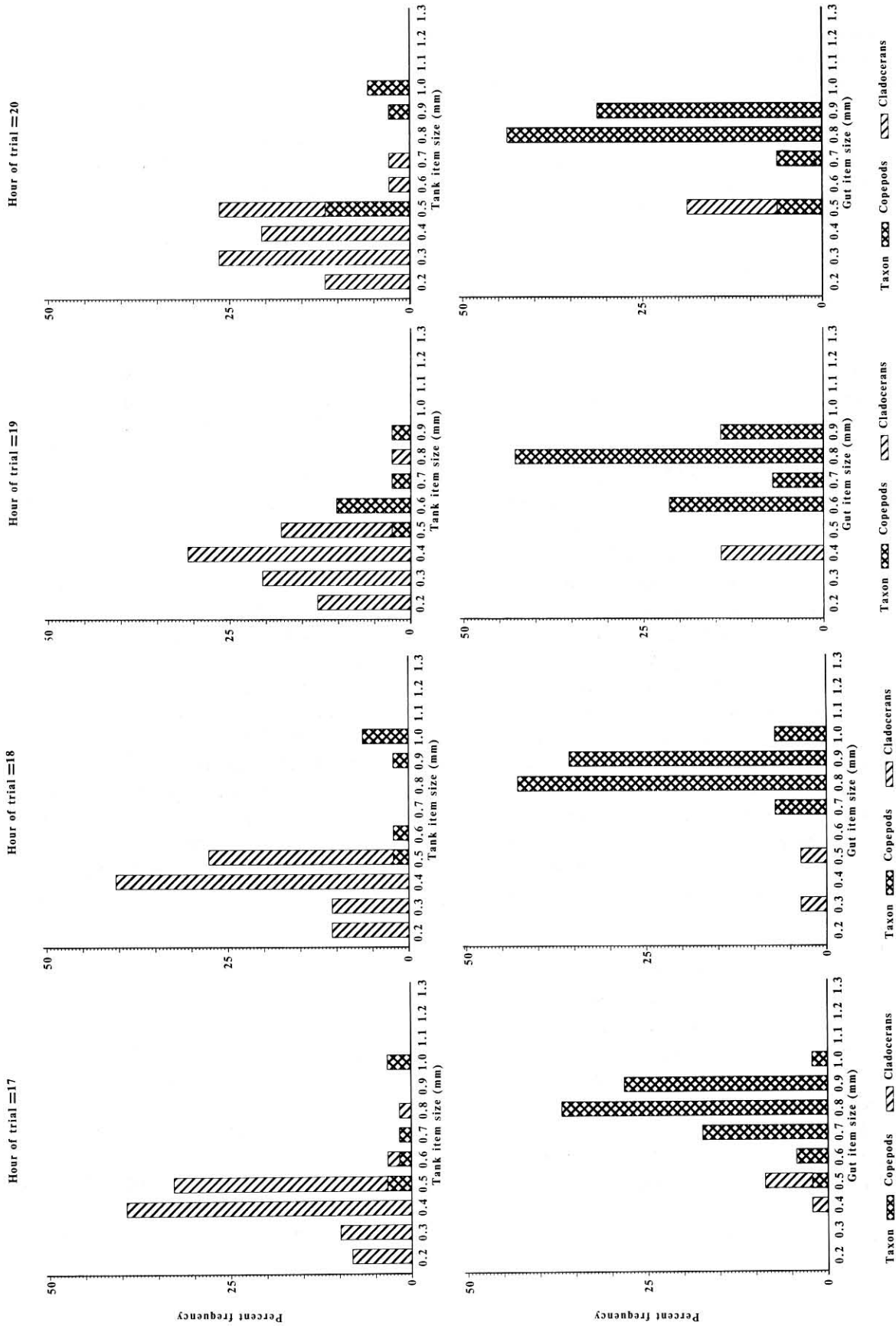


Fig. 8. Percent frequency histograms comparing the size frequency distributions of food items in the tank and in alevin guts for each hour analyzed. Data for each hour is lumped from the gut contents of 10 fish.

Table 4. Hourly summaries of the Standardized Forage Ratio index (SFR) for each 0.2 mm size interval of prey items available. Values $>1/n$ indicate preference, $<1/n$ avoidance.

Hour	0600	1000	1100	1200	1700	1800	1900	2000
1/n	0.17	0.20	0.20	0.25	0.20	0.20	0.25	0.20
SFR (.2-.3 mm)	0.005	0	0	0.04	0	0.004	0	0
SFR (.4-.5 mm)	0.003	0.006	0.009	0.14	0.003	0.001	0.02	0.02
SFR (.6-.7 mm)	0.005	0.03	0.01	0.19	0.09	0.08	0.16	0.04
SFR (.8-.9 mm)	0	0.07	0.08	0.63	0.89	0.89	0.82	0.94
SFR (1.0-1.1 mm)	0.33	0.90	0.90	-	0.02	0.03	-	0
SFR (1.2-1.3 mm)	0.66	-	-	-	-	-	-	-

evins had been without food for the 8 nocturnal hours immediately prior to the experiment, so that the pronounced early morning peak in activity was at least partially in response to an empty gut.

The pattern exhibited by Miss-spit, which was interpreted as an indicator of error in the feeding sequence, followed that of 'total activity'. As activity declined, error in feeding (and its associated variance) declined. The composite variables expressing feeding success (Success 1 and Success 2) also reflected this pattern; both declined with increasing activity. Bite/fix, which was interpreted as the likelihood that the fish would attack an item upon which they had visually fixed, was high in the first few hours of feeding; alevins attacked virtually everything upon which they visually fixed. High Bite/fix was associated with the peak in feeding error, the drop in both indicators of feeding success, the increased variability in selection for gross taxa and the reduction in the intensity of size selection. Also, as the likelihood of a bite-following-a-fix increased, the variance in this likelihood decreased.

In a study of the feeding habits of walleye larvae, Mathias & Li (1982) observed a three-peak diel pattern in feeding activity as well as a shift in the type of prey selected. Williams (1981), observed diel changes in the diets of Atlantic salmon alevins. A comparison of Figures 1 and 7 revealed a similar phenomenon; salmon alevins were less selective during their most active periods, indicating that diurnal rhythm in activity also affects prey selection.

It may be hypothesized that the accurate/effi-

cient performance of spatial tasks (e.g. estimation of prey distances, angles, sizes, shapes, motility patterns) by alevins is rhythmic. That (1) error in the feeding sequence (Miss-spit) carried lower variance when its mean value was low; (2) variance in feeding success (Success 2) declined when its mean value increased; and (3) intensity of size selection was inversely associated with 'total activity' may indirectly support this hypothesis. Recent studies on the neuroethology of feeding behaviour (Ewert et al. 1983, Ewert 1985, Marcotte & Browman 1986), the physiological ecology of sleep (Karmanova 1982) and the brain mechanisms of behaviour (Laming 1981) have begun to suggest the underlying causes of these rhythms and their implications for behavioural ecology. Because these processes exist in fish, in at least a phylogenetically precursive form (Allison & Twyver 1970, Broughton 1972, Tauber 1974, Karmanova et al. 1981, Shapiro et al. 1981, Karmanova 1982, Davis & Northcutt 1983), it would seem appropriate to introduce some of them here.

Karmanova et al. (1981) reported on the 24 h rhythm in sleep states of the catfish, *Ictalurus nebulosus*. Both day and night rhythms were characterized by a pattern of wakeful states followed by periods of sleep-like states (Fig. 9D). The 24 h pattern in catfish sleep-like states and heart rate reported by Karmanova et al. (1981) was offset by 30 min (because of differences in the time zone locations of the studies) and compared to the activity pattern reported here for Atlantic salmon alevins (Fig. 9). Low alevin activity occurred during periods corresponding to sleep-like states (and

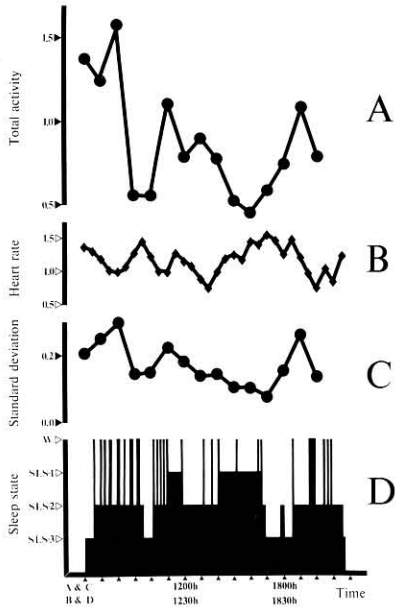


Fig. 9. (A) – The relationship between mean (for 10 fish) Total activity (# eye fixations + # moves + # Bites + # misses + # spits + # social + # ambiguous) per 3 minute observation period (normalized for tank zooplankton abundance) and time of day. SD = standard deviation (broken line) around the mean (solid line). The following hour pairs were statistically discernable, by multiple comparisons test, at the level of probability (P) indicated: 0600 and 0800 h vs 0900, 1000, 1500, 1600, 1700 h ($P < 0.01$); 0700 h vs 0900, 1000, 1500, 1600 h ($P < 0.06$); 0900 h vs 1100 h ($P < 0.08$); 1100 h vs 1500, 1600 h ($P < 0.05$); 1600 h vs 1900 h ($P < 0.06$). (B) – Diurnal periodicity in the heart rate of the catfish. Ordinate = time interval (seconds) between two subsequent heartbeats (redrawn from Karmanova et al. 1981). (C) – Variance in total activity (Fig. 9A) as represented by its standard deviation. (D) – diurnal periodicity in the wakefulness-primary sleep cycle of the catfish. SLS = sleep-like-state; SLS-1 = characterized by immobility with plastic muscle tone; SLS-2 = characterized by immobility with rigid muscle tone; SLS-3 = characterized by immobility with muscle relaxation; W = wakefulness (redrawn from Karmanova et al. 1981).

long intervals between heart beats); high activity during periods of wakefulness (shorter intervals between heart beats). Peaks in the variance of alevin ‘total activity’ (Fig. 9C) corresponded to intervals of rapid alternation between wakefulness and sleep in the catfish (Fig. 9D). Interestingly, there is evidence which suggests that activity rhythms in piscivores are the opposite of these of their planktivorous prey (Spencer 1939, Thorpe 1978, Federova & Drozhzhina 1982); piscivores, in general, are active immediately before dawn and

after sunset, the periods during which their planktivorous prey may be in sleep-like states.

In an examination of EEG’s from the optic tectum of a toad, Laming (1983) found that lower thresholds for neuronal discharge were associated with behaviourally active or aroused states and that these lowered thresholds enabled the animal to better detect and respond to environmental changes. Andrew (1983) and Andrew & Brennan (1983) reported right/left differences in the manner in which visual information was categorized in the brains of young chicks. Gur et al. (1982) have shown that verbal and spatial tasks in humans lead to increased blood flow to different cerebral hemispheres. Klein & Armitage (1979) have reported 90 to 100 minute oscillations in the performance of verbal and spatial tasks in humans. These oscillations were associated with lateral switching of the respective cerebral hemisphere which dominated observed behaviour (Gevins et al. 1983). This, in turn, has been linked to the REM/Non-REM rhythm in brain activity during sleep and its continuation during wakefulness, i.e. the Basic Rest Activity Cycle (BRAC) (Kleitman 1963, 1969, Jouvet 1973, Van Valen 1973, Broughton 1975, Klein & Armitage 1979). At certain points in the BRAC, performance of spatial tasks is enhanced, while at others spatial task performance is less effective. Processes such as these may well underly behavioural patterns such as those reported here for total activity, feeding error and feeding success.

Processes such as those discussed here are fundamental to an animals’ performance of cognitive (sensu Marcotte 1983) and spatial tasks, such as feeding, and should be more closely examined so that they can be incorporated into studies of behavioural ecology. Rhythms in perceptual and cognitive skills should be carefully considered in the scheduling of experiments and/or observations on fish feeding. Current models/ideas of fish feeding (e.g. Ware 1971, Milinski 1977, Confer et al. 1978, O’Brien 1979, Giguere et al. 1982, Hairston et al. 1982, Dill 1983, Ringler 1983, Dunbrack & Dill 1984, Wright & O’Brien 1984), though they have begun to consider the animals’ perceptual and cognitive abilities/limitations, may well benefit by proceeding these several steps further.

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