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Aggression, monopolization and growth depensation within groups of Japanese medaka (Oryzias latipes): interactions between the temporal and spatial clumping of food

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Abstract

Aggression, monopolization and growth depensation within groups of Japanese medaka (Oryzias latipes): interactions between the temporal and spatial clumping of food

Resource defence theory predicts that defence and monopolization increase as the spatial clumping, spatial predictability, and temporal predictability of resources increase and as temporal clumping of resources decrease. Previous tests of resource defence theory have manipulated only one aspect of resource distribution at a time. I tested whether there was an interaction between the effects of the spatial and temporal clumping of food by allowing groups of ten Japanese medaka (Oryzias latipes) to compete, over a 4 week period, for food in a 2 X 2 factorial design. As expected, the intensity of aggression increased as the spatial clumping of food increased and as the temporal clumping of food decreased. However, there was also a significant interaction between the effects of the spatial and temporal clumping of food on the intensity of aggression and total aggression. The number of fish in the feeding patch, a measure of monopolization, decreased as the spatial clumping of food increased, but was not affected by the temporal clumping of food. Although measures of aggression were high in the economically defendable trials, there was no apparent cost to resource defence, since mean growth rates did not differ significantly among treatments. Growth depensation increased over time, but was not influenced by the temporal or spatial distribution of food. The power of my experiment to detect a significant effect of food distribution on growth depensation was low. Therefore, although I failed to reject the null hypothesis, I cannot confidently conclude that the spatial and temporal clumping of food have no effect on the magnitude of growth depensation. My results suggest that care must be taken when extrapolating the results of single factor experiments to multi-factor or field situations.

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Introduction

An individual should defend a resource only if the net benefits of defence are greater than the net benefits of alternative behaviour patterns (Brown 1964). One of the key factors influencing the decision of whether or not to defend a resource is its distribution in time and space. Defence and monopolization are predicted to decrease as the temporal clumping of a resource increases (Trivers 1972; Emlen & Oring 1977; Wells 1977). When resources are temporally clumped, any time spent on defence is time away from resource exploitation. However, when resources are temporally dispersed, an individual may gain a larger portion of the resources if the time between the arrival of resource units is spent chasing competitors away. In contrast, defence and monopolization are predicted to increase as the spatial clumping of resources increases (Brown 1964; Trivers 1972; Warner 1980; Grant 1993). When resources are spatially clumped, defence is profitable because only a small area needs to be defended in order to gain access to a large portion of the resources. However, when resources are spatially dispersed, defence is uneconomical because a large area would need to be defended to acquire sufficient resources.

These contrasting predictions of the effects of the temporal and spatial clumping of resources on defence and monopolization have been largely supported by both field and laboratory studies (temporal clumping effect: Blanckenhorn 1991; Grant & Kramer 1992; Bryant & Grant 1995; and Grant et al. 1995; spatial clumping effect: Magnuson 1962; Monaghan & Metcalfe 1985; Grant & Guha 1993; Ryer & Olla 1995; Theimer 1987). The major limitation of such tests of resource defence theory is that they have considered only one factor of resource distribution at a time (Milinski & Parker 1991; Grant 1993).

In the wild, there is a well known positive correlation between the mean and variance (i.e. spatial clumping) of resource density (Green 1979; Gillis et al. 1986). It seems likely that similar correlations also occur between other measures of resource distribution (e.g. temporal clumping, spatial predictability, temporal predictability). If there are interactions between the various aspects of resource distribution, then the predictive power of resource defence theory would be limited. To date no study has simultaneously manipulated two or more aspects of resource distribution.

Aggression and resource monopolization are thought to lead to variation in body size within groups of individuals (Rubenstein 1981; Davis & Olla 1987). However, most studies of resource monopolization have been for short periods of time and have not linked aggressive behaviour and resource acquisition to longer term measures of fitness such as growth, fecundity and longevity (but see Bryant & Grant 1995). Within a cohort of growing individuals, it is common for skewness and variation of body size (length, weight, height) to increase over time (Uchmański 1985; Łomnicki 1988), particularly in fish populations which exhibit indeterminate (continuous) growth (Weatherley & Gill 1989; Magnuson 1962; Uchmański 1985; Koebele 1985; Elliott 1989; Beacham 1989; Jobling et al. 1993). This increase in variation of body size is known as growth depensation in the fisheries literature (Ricker 1958; Elliott 1989; Davis & Olla 1987; Ruzzante & Doyle 1990; Jobling et al. 1993). In aquaculture facilities, growth depensation leads to a few large, dominant fish and many smaller subordinates (Gunnes 1976; Jobling et al. 1993). Because of the potential link between resource monopolization and growth (Koebele 1985; Davis & Olla 1987), resource defence theory may be able to predict the magnitude of growth depensation.

The purpose of my study is to extend existing tests of resource defence theory in three important ways. First, I examine the temporal and spatial clumping of resources simultaneously to determine whether their effects on defence and monopolization are additive or interactive. Second, my experiments measure defence and monopolization over a longer period (28 days) than previous studies to determine whether the intensity of defence and monopolization of food have effects on the size variation within groups. Third, I determine whether resource defence theory can be used to predict the magnitude of growth depensation within a fish population.

I used juvenile Japanese medaka, Oryzias latipes, as my test animals because they compete aggressively for food (Magnuson 1962) and exhibit relatively fast growth (Ruzzante & Doyle 1990; Bryant & Grant 1995). I allowed 10 juveniles to compete for 28 days for food that arrived in one of four treatment combinations: 1) temporally dispersed, spatially clumped, 2) temporally dispersed, spatially dispersed, 3) temporally clumped, spatially dispersed, or 4) temporally clumped, spatially clumped. I tested five predictions of resource defence theory: (1) intensity of aggression increases as the temporal clumping of food decreases, (2) the intensity of aggression increases as the spatial clumping of food increases, (3) the effects of temporal and spatial clumping of food on intensity of aggression are additive, (4) monopolization of food increases as the intensity of aggression increases, and (5) growth depensation increases as the intensity of aggression and resource monopolization increase.

Methods

Experimental Animals

Japanese medaka are freshwater fishes (family Adrianichthyidae) which range in length from 2 to 4 cm at sexual maturity. Female medaka can potentially produce a single clutch of eggs (numbering 5 to 15) almost every day, given an appropriate photoperiod and diet (Yamamoto 1975). Two hundred medaka were purchased from a biological supply company in April 1995 and were kept in four, 95-l stock tanks at a sex ratio of approximately 2:3 (male:female). Initial photoperiod was 13:11 (light:dark) with dawn at 0800. In October of 1995, after two weeks of low reproductive activity, photoperiod was extended to 14:10 to stimulate further spawning. While in stock tanks, fish were fed daily with previously frozen brine shrimp (*Artemia* sp.), supplemented with TetraMin flake food for tropical fish.

Group Formation

I collected eggs from all females with clutches of eggs (i.e. approximately 15 females per day) for five consecutive days, approximately one month before the start of each experimental replicate. A five day period was sufficient to collect a large number (>750) of viable eggs. Females were captured using a clear watertight container; a dip net was not used because of potential damage to the eggs. Eggs were removed from the female's ventral surface by squirting them off with water using a glass pipette. The eggs were then allowed to water harden in a glass petri dish containing dechlorinated water and 1% methylene blue to inhibit fungal growth. Fertilized eggs were separated using fine forceps under a dissecting microscope, and 10 eggs were placed into a small 2.5 X 5 X 2.5 cm hatching container (one ice-cube tray cell) with a glass pipette. The methylene blue solution was replaced daily until eggs hatched approximately ten days later. The medaka larvae were then transferred with a pipette into a 6.5 l stock tank containing dechlorinated tap water and green algae. Fish fed on green algae for the first 1.5 weeks and were then fed ad libitum with brine shrimp nauplii (<u>Artemia</u> sp.) for the next 2.5 weeks.

I collected juvenile medaka from hatchery stock tanks one day before the beginning of the experiment and separated them into size classes ranging from 9 to 11 mm (± 0.5 mm). Standard length (mm) measurements (tip of snout to end of base of the hypural bones) were taken using a ruler under a dissecting microscope. Four groups of ten fish (40 fish per block) were formed so that the coefficient of variation (CV=[SD/mean]*100) of length within each group was zero (i.e. range in length <0.5 mm). In only one group was the CV of length not zero; it had a CV of length of 2.19. A total of 40 groups, ten per treatment, were used. Each group of ten fish was transferred to an experimental tank and randomly assigned to one of four treatments. Fish were not fed on this day.

Feeding Trials

I conducted experiments in 6.5 litre aquaria (30 x 12.5 x 17.5 cm), each equipped with an undergravel filter and light-coloured gravel to a depth of 3 cm. Filter tubes were covered with 1 mm^2 plastic mesh to eliminate accidental deaths. All experimental tanks were maintained at 22°C ± 1°C.

I manipulated the spatial and temporal distribution of food in a 2 X 2 factorial experiment so that resources were either dispersed or clumped in time as well as dispersed or clumped in space. Aquaria were covered with opaque Plexiglas lids into which either one hole was drilled (spatially clumped treatment) or one long slot was cut (spatially dispersed treatment). The hole for the spatially clumped treatment (1.0 cm in diameter) was positioned 4.5 cm from a corner of the lid, into which a funnel, with a mouth diameter of 5.3 cm and a tip diameter of 0.5 cm, was placed. The tip of the funnel extended through the lid and rested above a clear ring of 5.6 cm in diameter. Half the height of the ring (≈1.25 cm) was below the water level, and acted as a confinement area for the floating food items which were delivered into the funnel (Figure 1). A slot measuring 18.5

x 1 cm was cut into the centre of the lid for the spatially dispersed treatment, allowing the food items to be distributed across the surface of the aquaria (Figure 1). As a result, feeding patches in spatially dispersed trials were 15 times larger in both surface area and volume than feeding patches in spatially clumped trials (375.0 cm^2 vs. 24.6 cm^2 and 468.8 cm^3 vs. 30.8 cm^3, respectively).

I fed each group of 10 medaka once per day for 28 days (4 weeks). One minute prior to the feeding trial I shut off the air supply and added a drop of water to the experimental tank to serve as a cue to the fish that food was about to arrive. Throughout the experiment fish were fed TetraMin flake food. I fed each group of ten medaka 8% of their mean body weight per day multiplied by the number of individuals. I had previously determined a wet weight (g, Y) to standard length (mm, X) regression: $Y=0.006X-0.046$, ($r^2=0.928$, $N=60$). I also adjusted food flake diameter according to mean SL after each measuring session when necessary. Fish of 9-10 mm in length received ≈0.5-mm flakes, whereas larger fish received ≈1-mm flakes.

The total number of food items in the temporally clumped treatment was divided into 4 approximately equal rations; each ration was delivered at once (i.e. within a few seconds) at 2 minute intervals. Temporally clumped feeding trials were, therefore, approximately 8 minutes in duration. For the temporally dispersed treatments, the total amount of food was divided into 16 approximately equal rations; each ration was delivered over a 2 minute period, one food item every 10 seconds. Feeding trials for temporally dispersed treatments were approximately 32 minutes in duration. In the spatially clumped treatments, food items were dropped into the funnel and landed within the confinement area, whereas in spatially dispersed treatments, food items were dropped into the tank along the length of the slot in the lid and dispersed slightly on the surface of the water.

Growth Measurements

I took length measurements on day 0, 14 and 28 (day 0 being the day before feeding commenced), for a total of 3 size measurements for each treatment in all replicates. Final size measurements (day 28) consisted of length as well as wet weight to the nearest 0.001 g. I used wet weight instead of dry weight so that fish would not have to be killed at the end of the experiment. However, preliminary data showed that wet and dry weight measurements for medaka were highly correlated ($r=0.938$, $n=64$, $P<0.001$). Wet weights were not taken until the end of the experiment to avoid the stress associated with this procedure.

Growth depensation is usually measured as an increase in the coefficient of variation ($CV=[SD/mean]*100$) of length or weight over time (Brett 1979). Growth depensation for each treatment was calculated from the measurements of final weight and SL taken every two weeks.

Videotaping Procedures

To estimate resource monopolization and aggression, I videotaped feeding sessions from the front of the experimental tanks on days 6, 10, 17 and 24. I stood off to the side and delivered the food items while fish were monitored on a black and white monitor. Baseline levels of aggression were recorded by videotape on days 7, 11, 18 and 25, either two hours before or after fish had been fed in order to minimize potential aggression associated with feeding. All behaviour was retrieved later from videotapes.

Mortality

No fish died over the four weeks in 30 out of 40 aquaria. One fish died in 8 out of 40 aquaria and more than one fish died in two aquaria. Aquaria with more than 1 death were excluded from all analyses because of a potential inverse relationship between mortality and observed growth depensation (Elliott 1989). In addition, smaller group sizes could affect the potential for resource defence (Chapman & Kramer 1996) and confound the effect of the experimental treatments. To validate that even one mortality per aquaria did not affect results, treatments with zero mortality (n=30) were then compared with the results from tanks with one death (n=8). Results were qualitatively the same for all analyses so I presented results using all groups with one or no mortalities (n=38).

Data Analysis

My operational measure of intensity of resource defence was the total per capita chase rate in the feeding patch (chases in the patch/individual in the patch/min). A chase was defined as a short unidirectional burst of increased swimming directed at another individual. In order to be counted as a chase, the snout of either the chasing or the chased fish had to be in the patch at the initiation of the chase. I also quantified the total amount of aggression as the total number of chases in the feeding patch (number/trial), and non-feeding aggression as total per capita chase rate (chases in the aquarium/individual/min). Fewer than 5% of the aggressive interactions during feeding took place outside of the feeding patches and were, therefore, not considered further. I used the $\log_{10}$ transformation for these variables to meet the assumptions of parametric tests.

I did not directly measure food monopolization (e.g. CV of food eaten within groups) because fish were not individually marked. Instead, I used an indirect measure of monopolization, the percentage of fish in the feeding patch. In the spatially clumped treatments, fish were defined as in the patch when at least their snout was within the feeding ring. In the spatially dispersed treatments, an individual was considered in the feeding patch if it was in the feeding position (body at 30° angle) within one body length of the surface of the water. Percentage of fish in the patch was arcsine square root transformed to meet the assumptions of parametric tests.

In my attempt to minimize CV within groups, I inadvertently manipulated mean size of the fish among treatments (ANOVA: $F=48.9$, $df=3,34$, $P<0.001$; Figure 2). Hence, treatment and initial body size are confounded in my experiment. Because of the differences among treatments in initial body size, I included it as a covariate in most analyses. Treatment effects were only considered after the effects of initial body size were included in the model. Although this approach does not eliminate the confounding between initial body size and treatment, it does allow me to identify when apparent effects of the treatments are more likely an artifact of initial body size. ANCOVA results are reported only when the effect of initial body size is significant ($P<0.05$); otherwise I report the results of the two-way ANOVA.

To investigate the influence of the main effects on aggression and monopolization, I used a two-way repeated measures analysis of variance (ANOVAR). In addition, I used a simple two-way ANOVA using the average of the four weekly observations as the dependent variable. Because both analyses gave similar results, I report the results of the two-way ANOVA. However, for trends in aggression, monopolization, CV of length, and body length over time, I report the results of the repeated measures two-way analysis of variance. The Huynh-Feldt correction was used for all tests of within-subjects effects (Potvin et al. 1990).

I used the statistical package NCSS 6.0 (1995) for tests of normality (Martinez-Iglewicz test). To examine the final length and weight distributions, frequency distributions were constructed for all 38 groups of 9 or 10 fish. Furthermore, I examined final length and weight distributions for all fish in a treatment (N=98 or 100). For these combined distributions, I used standardized means (Z-scores) for each group of 9 or 10 fish in order to control for differences in final body sizes between groups. Trends in skewness, kurtosis, and overall normality were examined for all 38 groups and the combined distributions.

Results

Aggression

There was a significant interaction between the effects of the temporal and spatial clumping of food on the intensity of resource defence (ANOVA: F=19.40, df=1,34, P<0.001). The increase in aggression as food became less clumped in time was greater in the spatially dispersed than in the spatially clumped trials (Figure 3). However, the magnitude of both main effects were almost three times greater than the magnitude of the interaction effect and were, therefore, still meaningful (Snedecor & Cochran 1980). The intensity of aggression was higher when food was temporally dispersed than when temporally clumped (ANOVA: F=52.59, df=1,34, P<0.001). In contrast, the intensity of aggression was lower when resources were spatially dispersed than when spatially clumped (ANOVA: F=55.80, df=1,34, P<0.001). Both main effects are consistent with the predictions of resource defence theory.

Per capita chase rate during non-feeding periods was not significantly affected by the temporal (ANCOVA: F=3.37, df=1,33, P=0.07) or spatial (ANCOVA: F=0.48, df=1,33, P=0.49) clumping of food. In addition, the rate of non-feeding chases did not change significantly over the 28 days of the experiment (ANCOVAR: F=0.65, df=3,99, P=0.58). On average, the rate of aggression during non-feeding periods was much lower than during feeding trials (Figure 3).

There was also a significant interaction between the main effects of temporal and spatial clumping of food on the total number of chases during a feeding trial (ANCOVA: $F=23.05$, $df=1,33$, $p<0.001$; Figure 4). When food was temporally clumped, aggression was more frequent in the spatially clumped trials, but when food was temporally dispersed aggression was more frequent in the spatially dispersed trials. However, this interaction was overwhelmed by the effect of temporal clumping; on average, there were 7.3 times more chases in temporally dispersed trials than in temporally clumped trials (ANCOVA: $F=190.98$, $df=1,33$, $P<0.001$). The effect of temporal clumping was not surprising, because the duration of temporally dispersed trials was four times longer (32 min) than temporally clumped trials (8 min). However, aggression during the feeding period accounted for only 1.9 to 20.0% of the estimated total daily aggression in aquaria (Figure 5). Hence, the difference between the total number of chases in temporally dispersed and clumped treatments decreased from 7.3 times during feeding trials to only 1.1 times when estimated for a 13-hour day.

There was a 45.8% decrease in the per capita chase rate and a 42.5% decrease in the total number of chases per trial over the four week experiment (Figure 6, ANOVAR: $F=13.56$, $df=3,102$, $P<0.001$; not shown, ANOVAR: $F=10.50$, $df=3,102$, $P<0.001$).

Monopolization

Fewer fish were in the feeding patch during spatially clumped trials (35±2.7%) than during spatially dispersed trials (74.0±2.1%) (ANOVA: F=141.56,df=1,34, P<0.001; Figure 7). However, contrary to the predictions of resource defence theory, the number of fish in the feeding patch was not significantly affected by the temporal clumping of food (ANOVA: F=0.24, df=1,34, P=0.62). There was no significant interaction between the main effects of temporal and spatial clumping of food on the percentage of fish in the patch (F=2.20, df=1,34, P=0.15).

Over the four week experiment there was an interaction between spatial dispersion and time on the percentage of fish in the patch (ANOVAR: interaction between week and spatial clumping, F=3.811, df=3,102, P=0.013; Figure 8). The percentage of fish in the patch increased in the spatially clumped treatments but did not change in the spatially dispersed treatments.

Growth

Mean standard length increased significantly throughout the experiment (ANOVAR: F=2345.98, df=2,68, P<0.001; Figure 9). The initial size differences between temporally clumped and dispersed treatments persisted over the 4 weeks of the experiment (ANOVAR: F=33.965, df=2,68, P<0.001; Figure 9). When initial length was included as a covariate, there was no effect of the temporal (ANCOVA: F=3.05, df=1,30, P=0.09) or spatial (ANCOVA: F=0.11, df=1,30, P=0.74) clumping of food on final length.

Coefficient of variation of length increased over the 28 days of the experiment (ANOVAR: F=221.27, df=2,68, P<0.001; Figure 10). Coefficient of variation of body length in the temporally clumped trials increased significantly faster than temporally dispersed trials (interaction between week and temporal clumping, ANOVAR: F=7.2, df=2,68, P=0.002). Spatially clumped and dispersed trials did not differ significantly in the CV of body length (ANOVAR: F=0.39, df=2,68, P=0.62). After controlling for initial body size, the temporal and spatial clumping of food had no effect on the final CV of body length (ANCOVA: temporal F=0.281, df=1,33, P=0.600; spatial F=3.038, df=1,33, P=0.091). Similarly, CV of body weight was not significantly affected by resource distribution, after controlling for initial body size (not shown).

Skewness

None of the eight combined length or weight frequency distributions for each treatment were significantly different from a normal distribution (Martinez-Iglewicz test; P values >0.05). Only one out of 38 aquaria had a length-frequency distribution significantly different from normal and only three out of 38 aquaria had weight-frequency distributions that differed significantly from normal. Because two out of 40 distributions were expected to be significantly different from normality by chance alone, there was no compelling evidence of skewed size distributions in my experiment.

Discussion

As predicted, the intensity of aggression increased as the temporal clumping of resources decreased and the spatial clumping of food increased. My results are similar to those from earlier studies that manipulated only the temporal (Blanckenhorn 1991; Grant & Kramer 1992; Bryant & Grant 1995; Grant et al. 1995) or spatial (Magnuson 1962; Monaghan & Metcalfe 1985; Grant & Guha 1993; Ryer & Olla 1995) clumping of resources. However, there was a significant interaction between the effects of the temporal and spatial clumping of resources on the rate of aggression. Surprisingly, in the spatially clumped trials, the rate of aggression declined very little as the temporal clumping of food increased. The temporal dispersion of food may have had no effect because the food floated at the surface. Hence, dominant individuals within the spatially clumped patch may not have been forced to choose between feeding and defending; they could have chased competitors away from the patch and then returned to eat any accumulated floating food. In contrast, most other studies of temporal clumping have forced the dominant individuals to choose between acquiring an ephemeral resource item or chasing competitors (e.g. Blanckenhorn 1991; Grant & Kramer 1992; Bryant & Grant 1995; Grant et al. 1995).

The interaction between the temporal and spatial clumping of food had an even greater effect on total aggression than on the rate of aggression. In the temporally clumped trials, the total amount of aggression was actually higher in the spatially dispersed than in the spatially clumped trials. This surprising result occurred because the duration and number of individuals occupying spatially dispersed patches was greater than the duration and number of individuals occupying spatially clumped patches. These data point out the importance of considering an individual's opportunity to be aggressive when testing resource defence theory (see Grant & Kramer 1992; Grant & Guha 1993). Per capita rate of aggression is preferable to total aggression when testing the predictions of resource defence theory.

These interactions have implications for tests of resource defence theory. The effects of the spatial clumping of food cannot necessarily be predicted independently of the temporal clumping of food and vice versa. If this type of interaction occurs between other aspects of resource distribution that are correlated in the wild (e.g. mean density, spatial predictability, temporal predictability), then the predictive power of resource defence theory may be limited. Future studies of resource defence need to examine other potential interactive effects between aspects of resource distribution.

Total aggression during a feeding trial was 7.3 times greater when food was temporally dispersed than when temporally clumped. The magnitude of aggression that accompanies an extremely temporally dispersed resource may have energetic consequences for both dominant and subordinate individuals. For example, in lek mating systems with extended breeding sessions, males may not be able to maintain a central territory for the entire season (Campanella & Wolf 1974). Similarly, the feeding of fish throughout the day in aquaculture facilities may promote continuous aggression throughout the day, increasing the potential for fin damage (Abbott & Dill 1989) and physiological stress (Koebele 1985).

As predicted, monopolization of the food patch increased as the spatial clumping of food increased; on average, only three fish occupied the spatially clumped patches compared to seven fish in spatially dispersed patches. Presumably, dominant individuals were able to exclude subordinates from the spatially clumped patches. That only 3 fish occupied the spatially clumped patches was not due to a space limitation per se; many more fish typically crowded into these patches at the beginning of trials before dominant individuals were able to monopolize the patch. Surprisingly, monopolization of the food patch did not increase as the temporal clumping of food decreased, despite a dramatic increase in aggression. Aggression did not appear to be effective in excluding individuals from the spatially dispersed patch.

On average, fish grew 0.11 mm/day in my experiment compared to 0.059 mm/day in Ruzzante & Doyle's (1990) experiment. The lack of difference in growth rate among treatments suggested that the energetic cost of aggression was low. However, my ability to detect a cost of feeding-related aggression may be limited by the large amount of aggression that occurred outside the feeding trials. Many other studies have also failed to detect an energetic cost of aggression (Koebele 1985; Blanckenhorn 1992; Bryant & Grant 1995; but see Rubenstein 1981; Metcalfe 1986; Røskaft et al. 1986).

As was expected (Uchmański 1985; Łomnicki 1988), CV of body length increased over the four weeks of the experiment. Interestingly length and weight frequency distributions at the end of my experiment were almost always not significantly different from a normal distribution. In contrast, Uchmanski (1985) suggested that positively skewed distributions are the rule when growth variation occurs within groups (Gunnes 1979). Surprisingly, the spatial clumping of food had a significant effect on monopolization but not on the degree of growth depensation. My measure of monopolization may have overestimated the actual monopolization of food. Individuals may have "taken turns" cycling in and out of the feeding patch in the spatially clumped trials.

Previous single-factor manipulations of food have found significant increases in growth depensation as the temporal clumping of food decreases (Ryer & Olla 1996) or as the spatial clumping of food increases (Magnuson 1962; Davis & Olla 1987; Ryer & Olla 1995; Ryer & Olla 1996). For example, two studies produced differences in the CV of weight of 9 and 15% between treatments (Ryer & Olla 1995; 1996). An <u>a posteriori</u> analysis revealed that the power (i.e. the probability of correctly rejecting the H_o) of my experiment to detect a difference in CV of weight of 10% was 0.46 (calculated from Zar 1984). Hence there was a 54% chance of making a Type II error (ß) (i.e. wrongly accepting the H_o). Therefore, my experiment failed to reject the H_o, but I cannot confidently accept the null hypothesis with a power less than 0.8 (Peterman 1990).

In summary, my experiment has shown that resource defence increases as the temporal clumping of food decreases and spatial clumping of food increases. It is the first study to demonstrate an interaction with respect to aggression, between the distribution of food in time and space. There was an increase in aggression as food became less clumped in time that was greater in the spatially dispersed than spatially clumped trials. Future studies of resource defence need to examine other potential interactive effects between aspects of resource distribution.

Figure 1: Schematic diagrams illustrating the four combinations of temporal and spatial distributions of food: A) temporally dispersed, spatially clumped; B) temporally dispersed, spatially dispersed; C) temporally clumped, spatially dispersed; D) temporally clumped, spatially clumped.

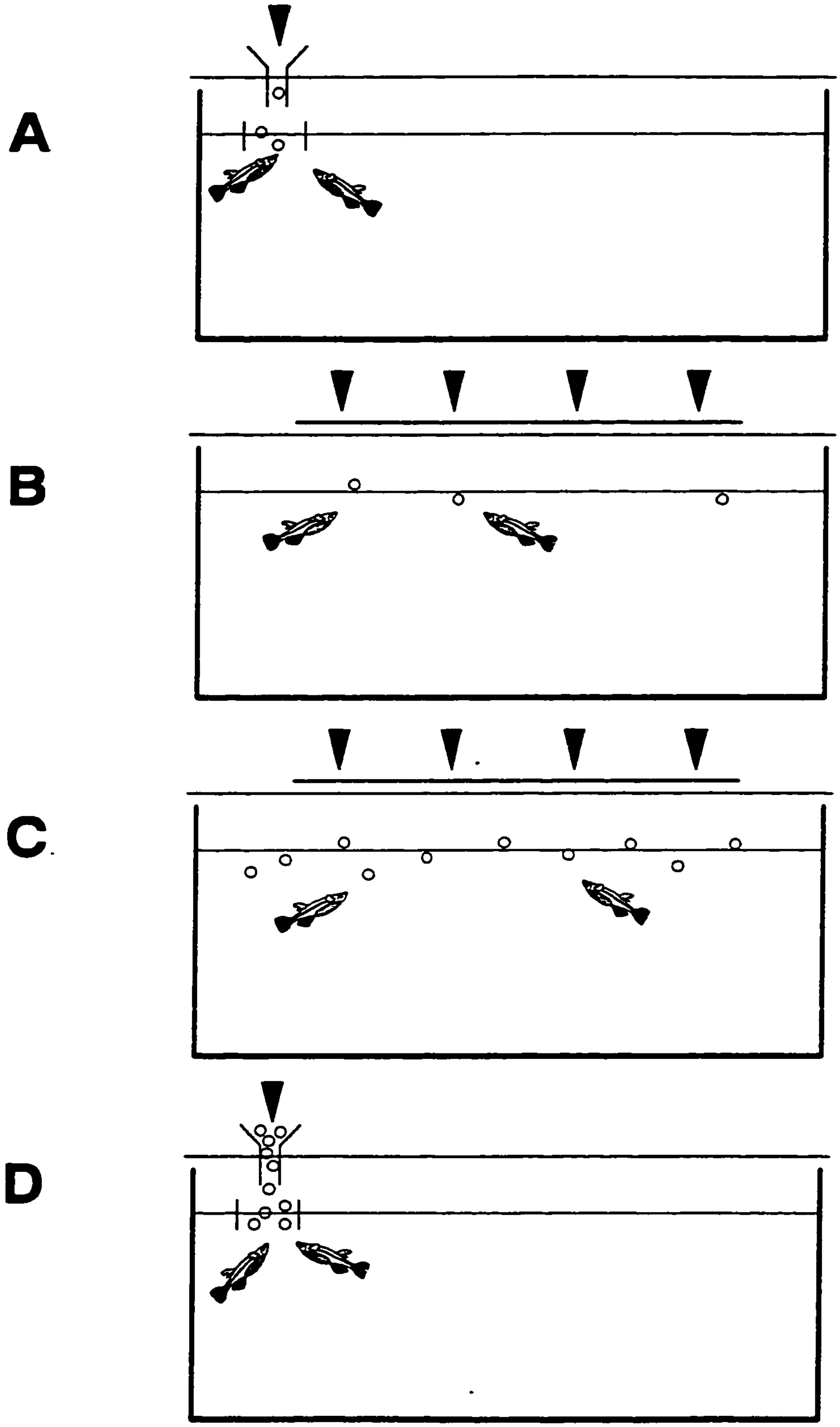

A
B
C
D

Figure 2: Mean (±1 SE, n=9 or 10) initial body length of groups of ten juvenile Japanese medaka and the treatment tanks to which they were assigned.

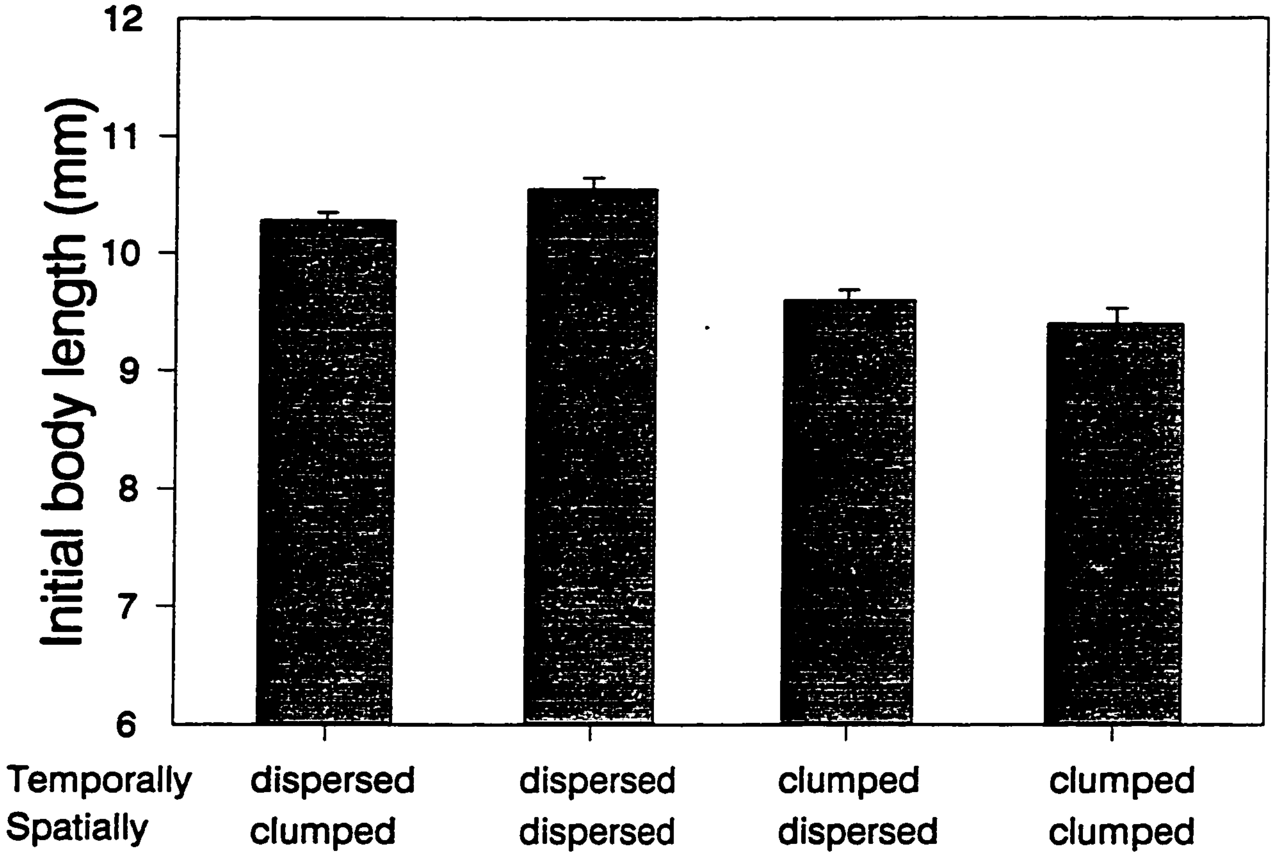
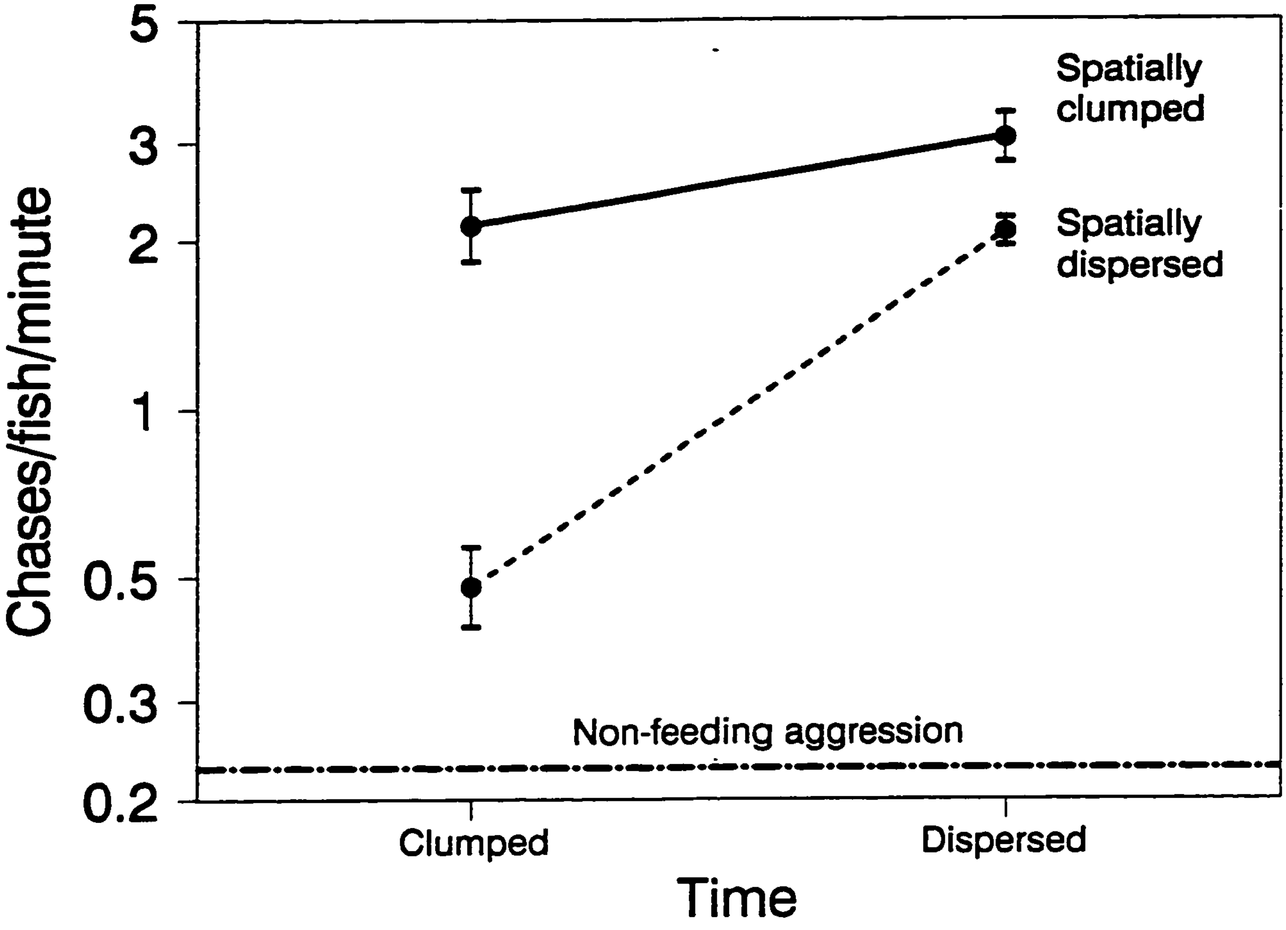

Initial body length (mm)
12
11
10
9
8
7
6
Temporally
Spatially
dispersed
clumped
dispersed
dispersed
clumped
dispersed
clumped
clumped

Figure 3: The effects of temporal and spatial distribution of food on the per capita rate of aggressive interactions in the feeding patch during feeding trials. Closed circles represent replicate means (±1 SE, n=9 or 10). The dash-dotted line represents mean aggressive interactions during non-feeding periods.


5
3
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0.3
0.2
Chases/fish/minute
Spatially clumped
Spatially dispersed
Non-feeding aggression
Clumped
Dispersed
Time

Figure 4: The effects of temporal and spatial distribution of food on the total number of aggressive interactions during a feeding trial. Closed circles represent replicate means (±1 SE, n=9 or 10).

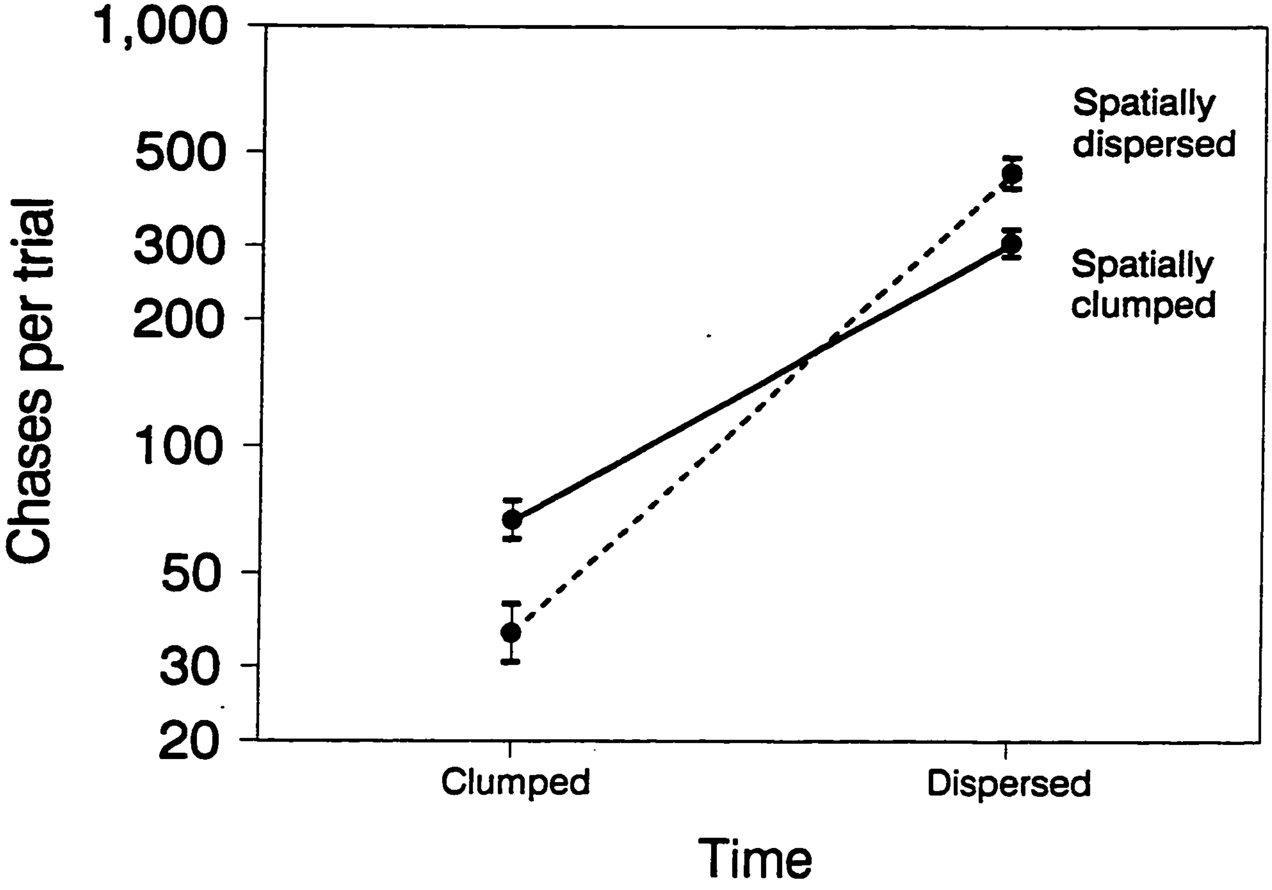

1,000
500
300
200
100
50
30
20
Chases per trial
Spatially dispersed
Spatially clumped
Clumped
Dispersed
Time

Figure 5: The total number of chases over a 13 hour day for each treatment. Open bars represent total aggression during non-feeding periods, extrapolated from the average chase rate for all treatments (Fig. 3). Shaded bars represent total chases during feeding periods per day that occurred during the feeding trials (percentage = number of chases during feeding trials / total chases pre day * 100).

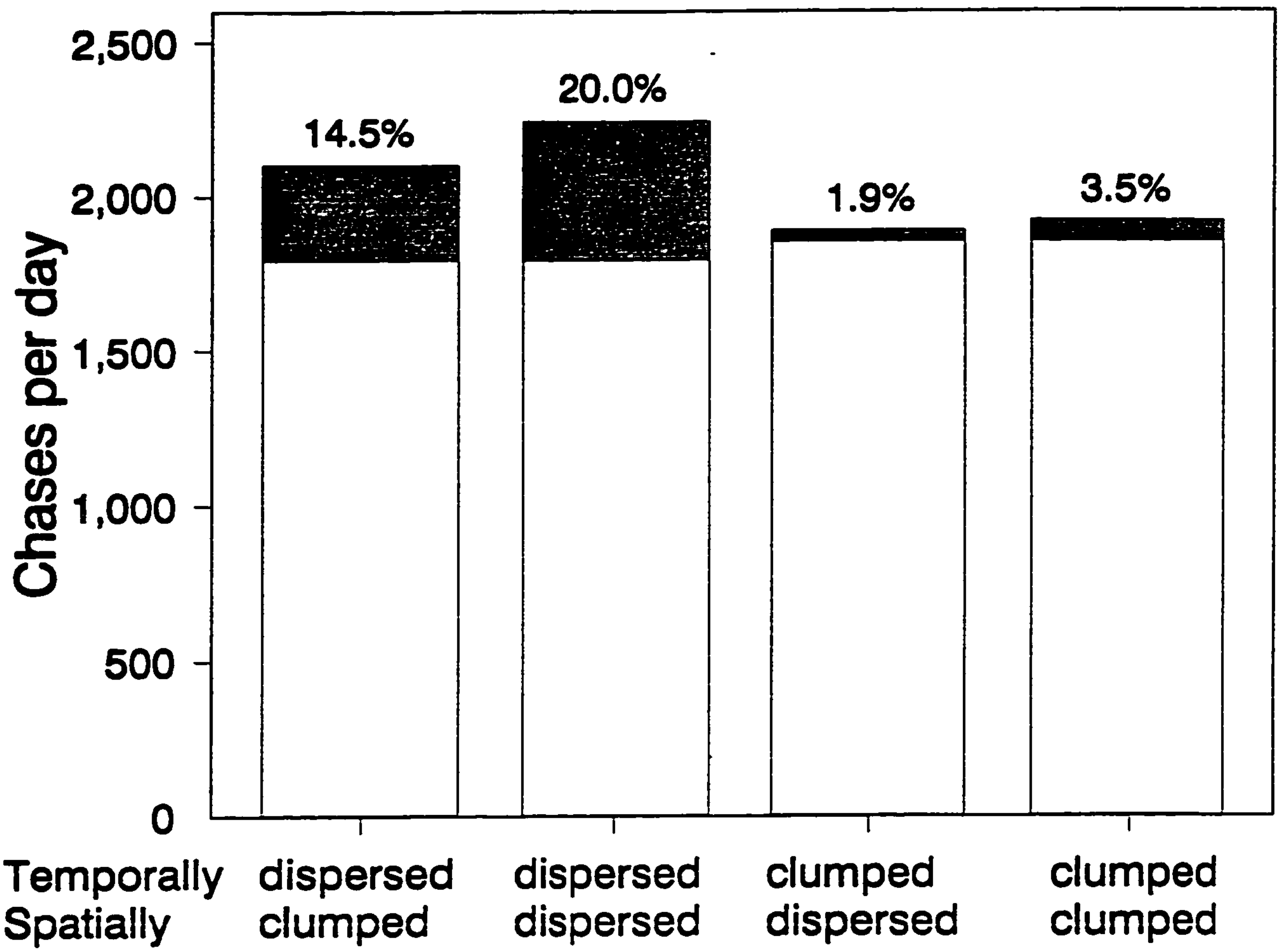

2,500
2,000
1,500
1,000
500
0
Chases per day
14.5%
20.0%
1.9%
3.5%
Temporally
Spatially
dispersed
clumped
dispersed
dispersed
clumped
dispersed
clumped
clumped

Figure 6: The effects of temporal and spatial resource distribution of food on the frequency of aggressive interactions during feeding trials over the four weeks of the experiment. Symbols represent replicate means (±1 SE, n=9 or 10). Closed circle = temporally dispersed, spatially clumped, open circle = temporally dispersed, spatially dispersed, open triangle = temporally clumped, spatially dispersed, closed triangle = temporally clumped, spatially clumped.

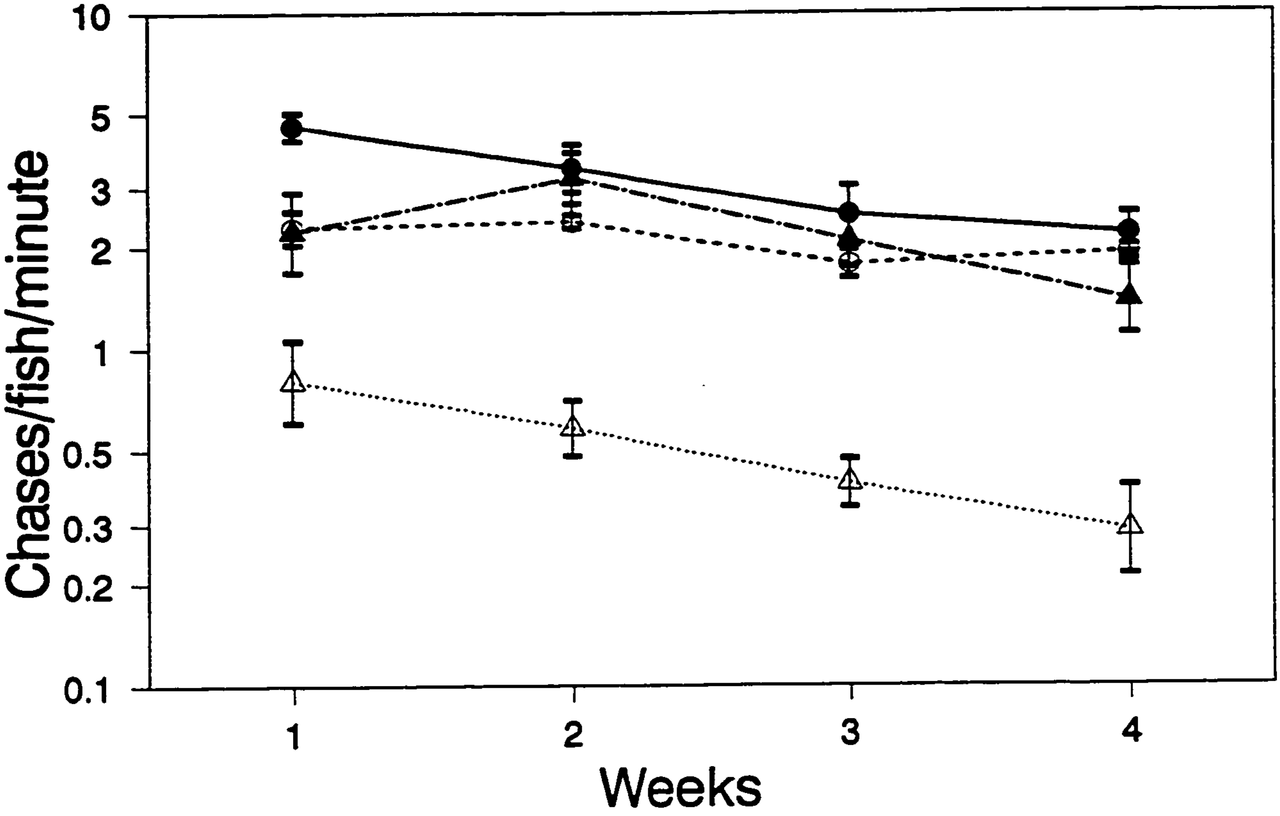

10
5
3
2
1
0.5
0.3
0.2
0.1
Chases/fish/minute
1
2
3
4
Weeks

Figure 7: The effects of food distribution in time and space on the percentage of ten juvenile Japanese medaka that were observed in the feeding patch. Closed circles represent replicate means (±1 SE, n=9 or 10).

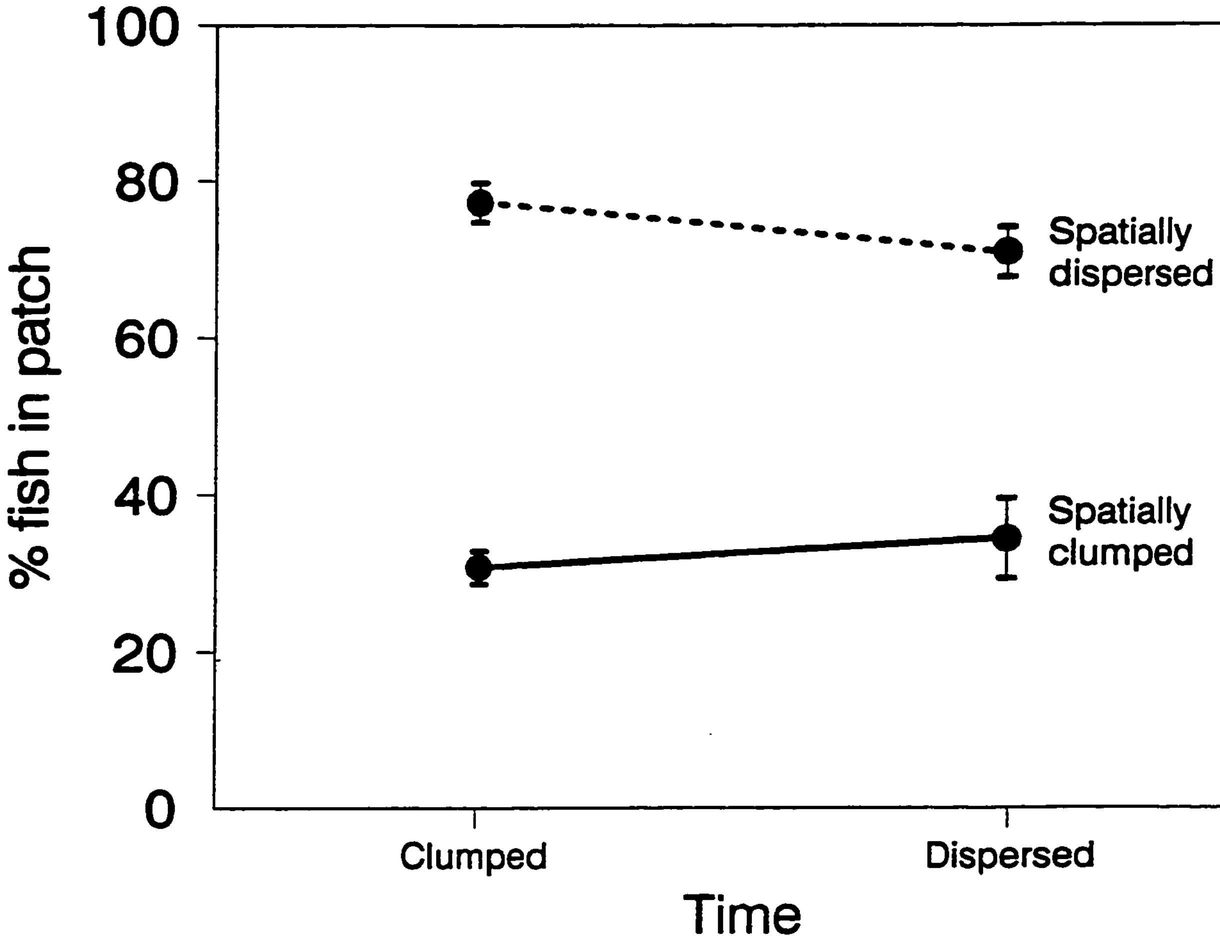

100
80
60
40
20
0
% fish in patch
Spatially dispersed
Spatially clumped
Clumped
Dispersed
Time

Figure 8: The effects of food distribution in time and space on the percentage of ten juvenile Japanese medaka in the feeding patch over the four weeks of the experiment. Symbols represent replicate means (±1 SE, n=9 or 10). Closed circle = temporally dispersed, spatially clumped, open circle = temporally dispersed, spatially dispersed, open triangle = temporally clumped, spatially dispersed, closed triangle = temporally clumped, spatially clumped.

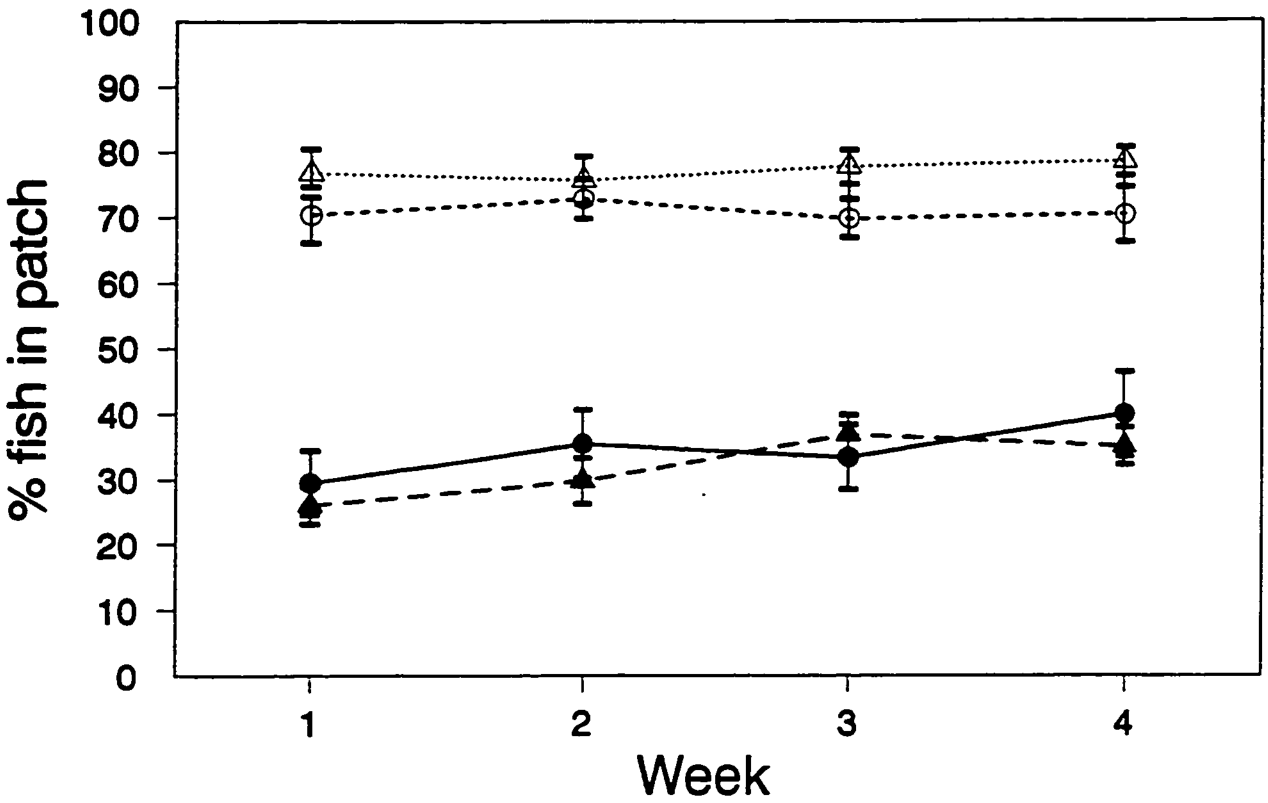

100
90
80
70
60
50
40
30
20
10
0
% fish in patch
1
2
3
4
Week

Figure 9: The effects of temporal and spatial distribution of food on the standard length (mm) of juvenile Japanese medaka throughout the four week experiment. Symbols represent replicate means (±1 SE, n=9 or 10). Closed circle = temporally dispersed, spatially clumped, open circle = temporally dispersed, spatially dispersed, open triangle = temporally clumped, spatially dispersed, closed triangle = temporally clumped, spatially clumped.

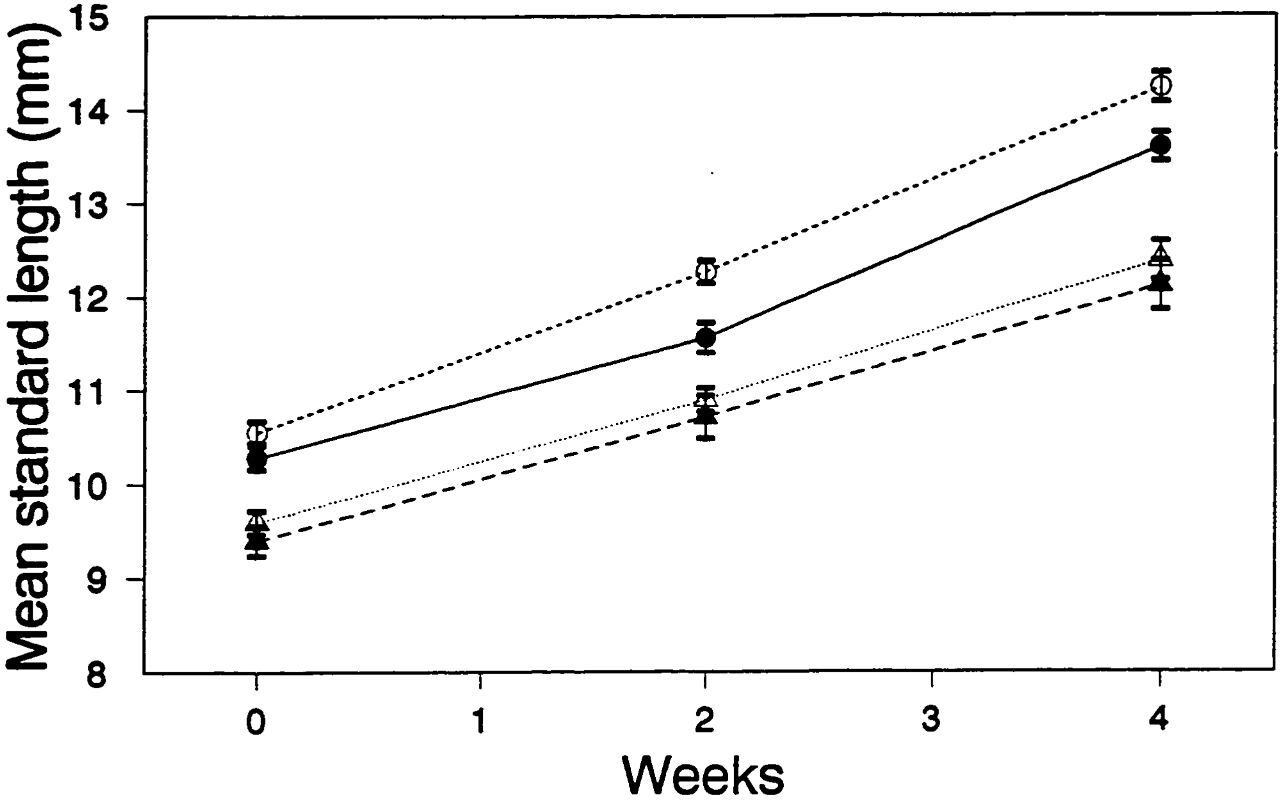
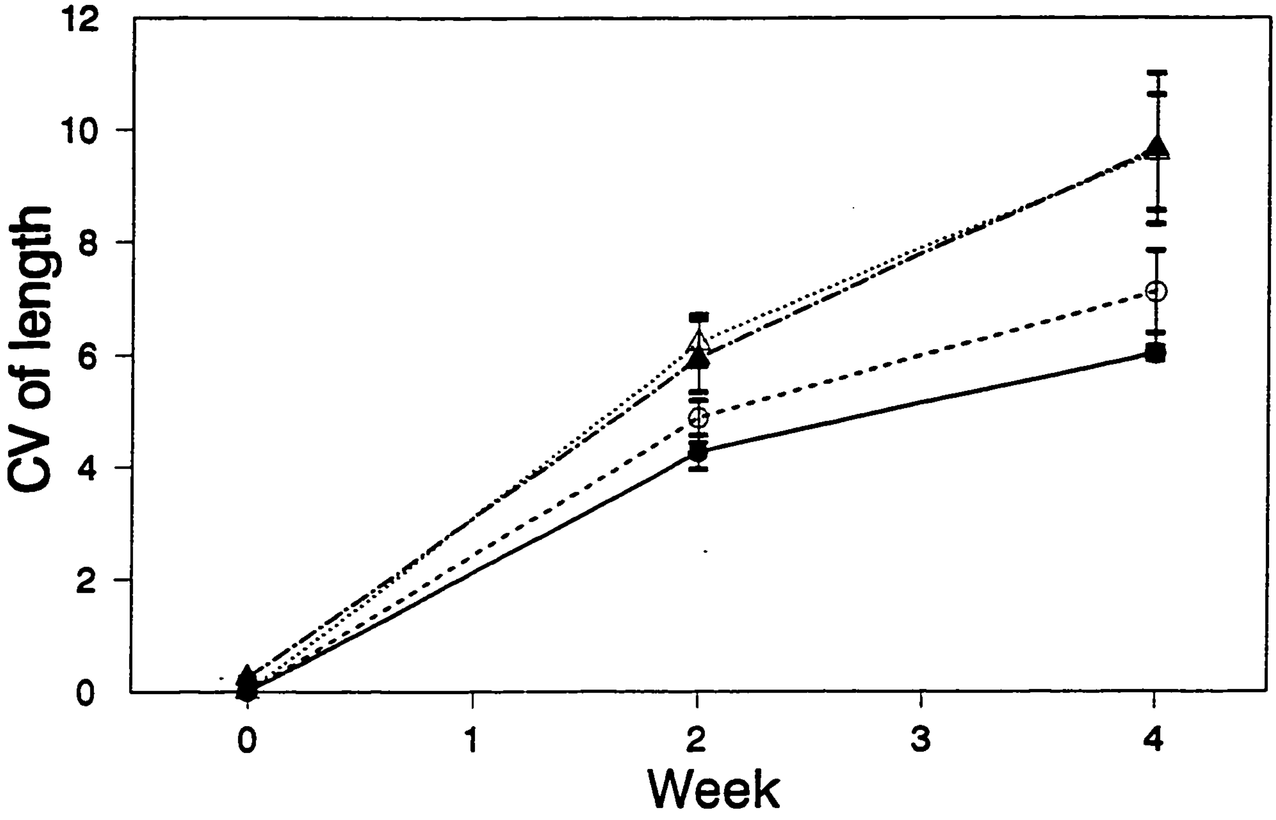

Mean standard length (mm)
8
9
10
11
12
13
14
15
0
1
2
3
4
Weeks

Figure 10: The effects of temporal and spatial food distribution on the CV of length of juvenile Japanese medaka over the four weeks of the experiment. Symbols represent replicate means (±1 SE, n=9 or 10). Closed circle = temporally dispersed, spatially clumped, open circle = temporally dispersed, spatially dispersed, open triangle = temporally clumped, spatially dispersed, closed triangle = temporally clumped, spatially clumped.


12
10
8
6
4
2
0
CV of length
0
1
2
3
4
Week

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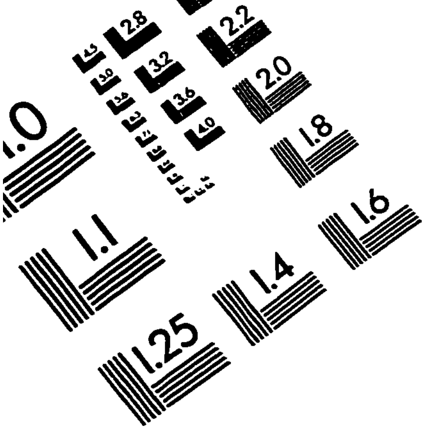

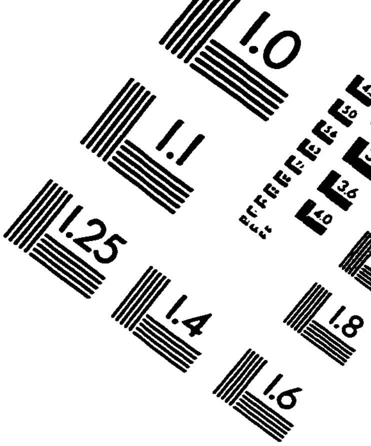

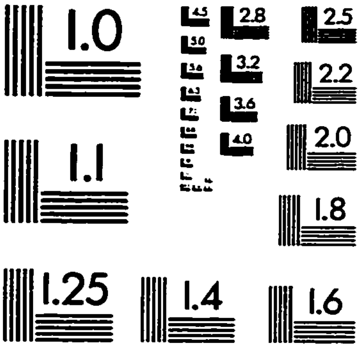

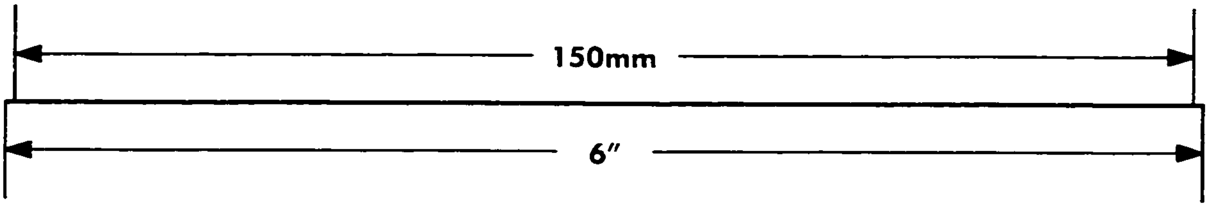

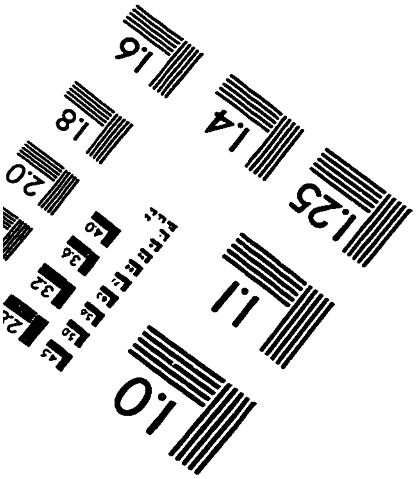

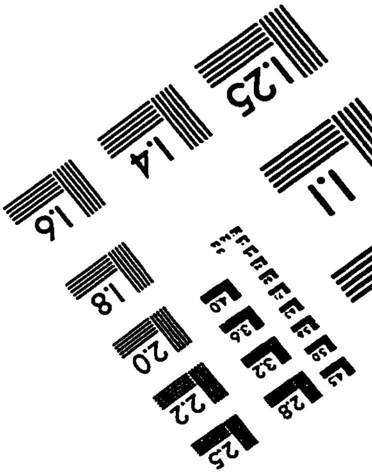

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