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Competition for food and variation of fitness in groups
of female Japanese medaka (Oryzias latipes)
depend on the synchrony of food arrival

Michael J. Bryant

A Thesis in
The Department of Biology

Presented in Partial Fulfilment of the Requirements
for the Degree of Master of Science at
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Abstract

Competition for food and variation of fitness in groups
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depend on the synchrony of food arrival

The distribution of resources in time is expected to influence how animals compete. Both aggression and resource monopolization are predicted to be higher when resources arrive asynchronously than synchronously. It is implicitly assumed that greater resource monopolization translates to greater variation in fitness, but this has never been demonstrated in a foraging situation. To test these predictions, groups of four female medaka (Oryzias latipes) were allowed to compete for a period of two weeks for brine shrimp (Artemia sp.) that arrived either synchronously or asynchronously. Fitness was measured as reproductive output, growth over the two week period, and surplus power, the sum of the energy allocated to reproductive output and growth. As predicted, both the monopolization of food and frequency of aggression were higher when food arrived asynchronously than synchronously. Variation of within-group fitness was also greater in the asynchronous than in the synchronous environment when measured by growth and surplus power, but not by reproductive output. These are the first results that test and support the prediction that fitness is more variable when food arrives asynchronously

than synchronously. Aggression was positively correlated with feeding success and ultimately to fitness in the asynchronous environment but was not correlated with either in the synchronous environment. My results suggest that food was economically defensible only in the asynchronous environment.

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Introduction

Competition for resources contributes to variation in fitness within groups. Not surprisingly, ecologists try to understand how and when organisms compete. One approach has been to examine how a resource's distribution in time influences both the intensity and outcome of competition for resources (Wells 1977, Trivers 1972, Emlen & Oring 1977, Grant 1993). When resources become available in unison they are described as synchronous, whereas resources that become available sequentially are distributed asynchronously in time.

The hypothesis that the temporal distribution of resources affects competition was initially proposed in the mating systems literature. Trivers (1972) hypothesized that the variation in mating success will be smaller when mates become receptive synchronously. When mates become receptive asynchronously, dominant individuals can potentially compete for each mate. Similarly, Emlen and Oring (1977) related the environmental potential for polygamy to the asynchrony of mates. When potential mates become receptive asynchronously they are more easily defended, allowing competitive individuals to monopolize a greater share. Wells (1977) predicted a switch from scramble competition to resource defence as the arrival of mates becomes more asynchronous.

Initially, only the temporal distribution of mates was considered, however the theory is also applicable to food. Blanckenhorn's (1991a) heuristic model predicted that the foraging success of dominant individuals will be less when the arrival rate of food is higher than the handling time (i.e. relatively synchronous). The influence of average, variance and skew of resource arrival rate have been formalized by Blanckenhorn and Caraco (1992). Milinski and Parker (1991) predict that interference competition will be associated with asynchronous food resources while scramble competition will be associated with synchronous food resources. Thus the "synchrony hypothesis" makes two general predictions concerning the competition for either mates or food. First, resource monopolization is predicted to be higher when resources are asynchronous than synchronous. Second, animals are predicted to gain resources through interference competition when resources are asynchronous and through scramble competition when synchronous.

Experimental tests of the synchrony hypothesis have shown increased resource monopolization with increasing asynchrony of food (Blanckenhorn 1991a, Grant & Kramer 1992). Only one study has demonstrated an increase in aggression or resource defence when resources become more asynchronous (Grant & Kramer 1992). In addition, both studies looked only at short term resource monopolization

and only at the gross benefits.

Brown's (1964) theory of economic defendability emphasizes the distinction between gross and net benefits. According to this theory, an animal will only defend a resource if the benefits of defence exceed the costs (i.e. positive net benefits). The economic defendability of a resource is often inferred by measuring separately the costs and the benefits of defence (Gill & Wolf 1975, Carpenter & MacMillen 1976). A more direct approach is to measure the net benefits, fitness being the ultimate net benefit of competition.

A correlation between foraging success and fitness is often assumed but rarely demonstrated (Blanckenhorn 1991b). However, the validity of this assumption depends on the costs of aggression. If there is a significant energetic cost of aggression and if aggression is used as a means of acquiring a greater percentage of food, then the correlation between feeding success and fitness may be zero or even negative. With respect to the synchrony hypothesis, a significant cost of aggression may reduce the variation in fitness when resources arrive asynchronously.

Surplus power, energy from assimilated food not used for the maintenance of the soma or for behavioural activity, (Ware 1982) provides a method for directly measuring the net benefits of competition for food. Because surplus power is used by an individual for a combination of growth and

reproduction, natural selection is expected to maximize the rate at which an individual gains surplus power (Ware 1982). Surplus power for animals such as teleosts, is an effective measure of fitness because it accounts for both future (growth) and present (reproduction) fitness components.

The purpose of my study is to test the two general predictions of the synchrony hypothesis in a foraging situation. My study extends the existing results in three important ways. First, I measure the gross gain of resources over a longer period. Second, I measure fitness using reproductive output, growth, and surplus power, allowing me to test the hypothesis that variation of fitness within groups is higher for groups fed asynchronously than synchronously. Third, I relate individual behaviour within a competitive environment to fitness.

I used groups of four female Japanese medaka competing for previously frozen brine shrimp. Medaka are known to compete aggressively for food in the laboratory (Magnuson 1962). The shrimp were presented either synchronously or asynchronously by manipulating their arrival rate. Each experimental group was fed at one level of synchrony for 14 days. Surplus power is easy to measure in female medaka because both growth and reproductive output are quantifiable and can be converted into energetic equivalents.

Methods

Japanese medaka are small, sexually dimorphic killifish (Oryziidae). Females have the potential to spawn daily given the appropriate photoperiod and diet. The spawning female extrudes a clutch of up to 50 eggs that remain attached to her ventral surface for a few hours. My experimental stock was shipped from Japan via a biological supply company in May 1992. Stock tanks (70 l) were maintained with an approximate sex ratio of 1:2 (male:female) at a density of 80 fish. The initial photoperiod was 14:10 (light:dark) with dawn at 07:00h. This photoperiod was extended to 18:6 in November 1992 to stimulate further spawning after several weeks of very low reproductive activity. While in the stock tanks, the fish were fed "Tetramin Flake" food and previously frozen brine shrimp (Artemia sp.) daily.

Experimental tanks

Experimental tanks (Fig. 1) measured 60 x 30 x 28.5 cm (l x w x h). Opaque black plastic dividers partitioned the tank into three compartments. Compartment one (60 x 5 x 28.5 cm), along the back of tank, contained a submersible heater, two undergravel filter stalks with air stones and tubes for the food delivery system. The second compartment, or feeding chamber (40 x 25 x 28.5 cm), contained a central feeding platform (13 x 4 x 4 cm) emerging from compartment

one, beige gravel to a depth of 3 cm, and a vertically sliding door (8 x 8 cm) into the third compartment. Compartment three, the spawning chamber (20 x 25 x 28.5 cm), had an opaque black plastic bottom instead of gravel, to facilitate egg collection. All experimental tanks were maintained at 28°C.

The food delivery system consisted of a peristaltic pump with Noroprene (size 25) tubing. Water from compartment one was pumped into an open funnel 15 cm above the water level. Food items could be dropped into the funnel where gravity would carry the food and water through a similar tube to the feeding platform. A 1-cm clear glass pipette protruded vertically from the feeding platform. Food items would gently float up from the pipette and, if uneaten, remain suspended for up to 30 s before falling to the gravel. A black plastic blind prevented the fish from seeing when food was put into the funnel.

Group formation

Approximately one week before an experiment began, several females in reproductive condition were transferred into the feeding compartment of a spare experimental tank. These fish were isolated from males and fed previously frozen brine shrimp ad libitum for five to nine days. During the morning that a group was to be formed, females

were sequentially presented to a single male, (see spawning section for details) until between five and eight females had spawned. These females were then individually held in 2 l beakers until they could be measured for wet mass and total length. Four of these females were chosen for an experimental group. A total of 56 females were used in the experiment (seven groups of four females for each of the two treatments).

To ensure that group composition was similar in both treatments, females were chosen to equalize both within-group mean body size and within-group variation in body size between treatments (means \pm SD of average group mass: synchronous = 355.25 mg \pm 64.81, asynchronous = 355.07 mg \pm 53.63; within-group CV of body mass: synchronous = 0.114 \pm 0.061, asynchronous = 0.121 \pm 0.052). The females were randomly assigned one of four locations for a subcutaneous injection of India ink. The marked fish were then placed in a clean experimental tank. The remaining unmarked fish were kept in another clean experimental tank for use as replacements for any fish that did not recover from the marking process by the next day. A total of three fish, out of 56, were replaced on the day after marking because of fungal infections or poor marks.

To ensure that all the females had a similar hunger level at the beginning of the experimental feeding sessions, they were starved for 60 h, beginning the night before the

group was formed. To minimize differences in reproductive state, each female was given one more opportunity to spawn on the morning before the first feeding session.

Spawning procedures

A male from a unisex stock tank was placed in the spawning chamber between 7:00 and 8:00 h. Each male was used only once per experimental group. Females were sequentially coaxed, with a dipnet, from the feeding chamber through the sliding door into the spawning chamber. To control for any potential effect of order of presentation to the male, the marked females were assigned to each of the four possible orders twice. Females were removed after a successful spawning or after 30 min. Females that spawned had an average latency of 8.78 min (range: 39 s to 30 min). Typically, males would vigorously court females even if they did not spawn. If a male did not court any of the females, (five out of 112 spawning trials), he was replaced and the whole process repeated. The same ordering of the females was used, but females were only given 15 min to spawn.

After a successful spawning, females were removed from the spawning chamber with a water-tight clear plastic basket. Any eggs eaten by either the male or the female were noted. Eggs that fell from the female's ventral surface were easily collected from the black plastic bottom

of the spawning chamber. The remaining eggs were removed from the female's ventral surface by squirting them off with water and a pipette or by brushing them off with a small paint brush. Females that did not spawn were removed from the tank and treated in the same manner as those that spawned to ensure all fish experienced a similar amount of handling stress. Females were given the opportunity to spawn seven times during the 14 day period of experimental feeding: prior to feeding sessions 5, 9, 13, 17, 21, 25, and immediately prior to being measured for the final time.

Feeding trials

One minute prior to the feeding trial, the peristaltic pump was turned on and air bubbles were pumped through the feeding tube for a few seconds. Thirty two previously frozen brine shrimp were individually dropped into the funnel. Food arrived at an average rate of one shrimp per 5s in the synchronous treatment and 1 shrimp per 60s in the asynchronous treatment. I varied the average arrival interval by $\pm 40\%$ of the average using a random uniform distribution. This ensured that fish could not predict the exact arrival time of a given food item. Unique feeding schedules were generated for each feeding session.

Experimental groups were fed twice daily, once between 11:00 and 13:00h and again between 19:00 and 21:00h. Each group

was fed a total of 28 times.

Videotaping procedures

To estimate resource monopolization and aggression, experimental groups were videotaped during feeding sessions 3, 7, 11, 15, 19, 23 and 27. Baseline dominance rankings were estimated prior to each taped feeding session. Dominance rank was calculated following Rubenstein (1981). Focal observations of each fish were made for two min, beginning 20 min prior to the beginning of the feeding session. All chases involving the focal animal were recorded on a small tape recorder. Within each dyad, the most aggressive fish was given a score of +1 while the subdominant was given a score of -1. In the case of a tie or when no interactions were observed for a dyad, both fish received a score of 0. The sum of the three dyad scores for each fish was then ranked so that the most aggressive fish was ranked 1.

Feeding sessions were filmed with a Super-VHS video recorder with an audio track. An assistant operated the food delivery system while I observed the fish. The identity of the fish chasing and eating was recorded on the audio track whenever possible. Missed behaviour could be retrieved later from the video tape. The pump was turned off one minute after the last shrimp was delivered.

Data Analysis

To quantify monopolization of food, I used three measures. The coefficient of variation (CV = standard deviation / mean * 100) of feeding success takes into account the distribution of ingested food items among all individuals in the group. The CV of feeding success was Log_{10} transformed to meet the assumptions of parametric statistical tests. The percentage of shrimp ingested by the most successful and least successful fish also indicates the unevenness of the distribution of food within a group. The angular transformation was used on these variables.

To test the prediction that aggression was higher in the asynchronous environment, total chase rate (per min) during the feeding trial was used. A chase was defined as a unidirectional burst of swimming oriented toward a conspecific. Because there were no chases in some feeding sessions for some or all of the fish within a group, the $\text{Log}_{10} (X + 1)$ transformation was used to meet the assumptions of parametric statistical tests. Comparisons of aggression and food monopolization between environments were made with repeated measures analysis of variance (ANOVAR). The Huynh-Feldt correction was used for all tests of within-subjects effects because compound symmetry could not be assumed (Potvin et al. 1990).

The observed CV of feeding success was compared to the

expected CV generated with a multinomial distribution (Grossman & Turner 1974). For the null distribution, each fish was assumed to have a 0.25 probability of ingesting any given shrimp and that a total of 32 shrimp were eaten per session. I calculated the CV and the probability of occurrence of all possible permutations of dividing 32 items among four individuals. From these statistics I constructed the probability distribution of finding a CV equal to or greater than the observed CV by chance.

Three measures of fitness were measured. Reproductive output (RO) was the sum of all eggs produced over the two week experimental period. Second, growth rate was calculated as the difference between initial and final wet mass. Third, to take into account individual differences in the partitioning of energy into eggs and somatic tissue, surplus power was calculated. Wet mass of medaka were translated to calories using the equation:

$$\text{Calories} = 0.875(\text{wet mass in mg})^{1.099}$$

($r^2 = 0.88$, Kaufman and Beyers 1972). Initial and final wet mass were converted to calories and then converted to joules by multiplication by the constant 4.1841. The average energetic value of a single medaka egg is 4.64 joules (Hirshfield 1980). An individual's surplus power was calculated as the change in energetic value of the carcass (final - initial) plus the energetic value of all eggs produced. Surplus power is expressed as energy * time⁻¹

(Ware 1982), in this experiment the units are joules per 14 days. Hirshfield (1980) used a similar measure called net production energy. Positive surplus power indicates a net gain in energy while negative surplus power indicates that the individual expended more energy than it assimilated from food. Within-group variation in RO, growth and surplus power were quantified in three ways. The within-group CV of RO, growth and surplus power were used as general measures of the within-group variation. In addition, the fish with the highest and lowest RO, growth and surplus power per group were compared between treatments. Comparisons of RO, growth and surplus power between the two environments were made using the Chi-square approximation of the Kruskal-Wallis test adjusted for a one-tailed test (SAS Institute 1985). One-tailed tests are appropriate because the synchrony hypothesis predicts that the variation in fitness will be greater in the asynchronous than in the synchronous environment.

Spearman rank correlations (r_s) were used to determine the relationship between pre-trial dominance, aggression and feeding success. Average feeding success and chase rate were calculated for each fish. Average dominance rank was calculated by pooling daily dominance rankings from the seven pre-trial feeding sessions that were videotaped. In all cases, variables analyzed with r_s were ranked within groups to control for differences between groups. The Chi-

square approximation of the Kruskal-Wallis test was also used to determine if relative feeding success was different for individuals with different relative frequencies of aggression. Partial correlations were used to determine if feeding success was related to fitness and if there was an energetic cost of aggression.

Results

Monopolization of food

As predicted, there was greater monopolization of food in the asynchronous environment compared to the synchronous environment (Fig. 2). Food was more unevenly distributed (higher CV) among individuals within a group when food arrived asynchronously (ANOVAR, $F_{1,12} = 44.05$, $P < 0.0001$). The fish with the highest feeding success in the asynchronous environment ingested a greater percentage of the shrimp compared to similar fish in the synchronous environment (mean \pm SD: asynchronous 46.08 ± 9.62 , synchronous 36.82 ± 6.37 ANOVAR, $F_{1,12} = 16.91$, $P = 0.0014$). Similarly, the fish with the lowest feeding success ingested only 3.18 ± 4.58 (mean \pm SD) percent of the shrimp per feeding session in the asynchronous compared to 13.18 ± 5.29 percent in the synchronous (ANOVAR $F_{1,12} = 21.29$, $P = 0.0006$).

The degree of monopolization tended to decrease with experience (Fig. 2, $F_{6,72} = 2.22$, $P = 0.08$). This effect may be due to the higher CVs on the first videotaped feeding session because some groups had not yet acclimatized to the feeding procedure. The effect of experience disappeared when the only the last six videotaped feeding session were analyzed ($F_{5,60} = 1.55$, $P = 0.195$).

The ranking of individual feeding success was significantly concordant ($P < 0.05$; Wilkinson 1990) over the two weeks in six of the seven asynchronous group (mean Kendall's $\tau = 0.638$, range 0.106 to 0.790), but in only two of the seven synchronous groups (mean Kendall's $\tau = 0.299$, range 0.031 to 0.639). To estimate individual feeding success over the 14 day experiment, the number of prey eaten by each individual was summed over the seven videotaped feeding trials (Fig. 3). As with the daily estimates of food monopolization, the CV for total food intake within groups was greater in the asynchronous than in the synchronous environment ($F_{1,12} = 14.88$ $P = 0.0023$). Because of the inconsistency of feeding success over time, the mean CV of total feeding success (23.52) was lower than the mean of the daily CV of feeding success (42.92) for the synchronous groups. In the asynchronous treatment, these two measures were similar (63.82 vs 76.65).

The within-group CV of feeding success was compared to the expected multinominal distribution assuming all fish

were equal competitors. On average 31.77 (SE = 0.095, minimum 27) shrimp were ingested per feeding trial. The probability of finding a CV equal to or greater than the CV observed from each videotaped feeding session was used in a combined probability test (Sokal and Rohlf 1981). When food arrived synchronously the CV of feeding success was higher than expected by chance in only eight of the 49 feeding sessions. These feeding sessions tended to be in the first half of an experiment (videotaped sessions 1 to 3). The combined probability, however, indicated that resource monopolization was still higher than expected by chance (combined probability test $\chi^2_{98} = 194.47$ $P < 0.001$). This effect disappears when videotaped sessions four to seven were analyzed separately (combined probability test $\chi^2_{56} = 67.30$ $P > 0.10$). The unevenness of the distribution of shrimp among individuals in the asynchronous environment was greater than expected by chance in 42 of the 49 videotaped feeding sessions (combined probability test $\chi^2_{98} = 636.29$ $P < 0.001$).

Because there were significant inconsistencies in feeding success in the synchronous environment, I compared the CV of total feeding success to the expected CV assuming equal competitors. The distribution of shrimp among individuals over the two weeks was significantly less variable than expected by chance (Fig. 3, combined probability test $\chi^2_{14} = 25.72$, $P < 0.05$). Not surprisingly

the observed CV of feeding success was higher than expected by chance in the asynchronous environment (combined probability test $\chi^2_{14} = 62.73$, $P < 0.001$).

Aggression and dominance

During feeding sessions, all fish in the synchronous groups congregated around the feeding platform. When chases occurred they were typically short and both the aggressor and the subordinates immediately returned to feeding platform. Aggression in the asynchronous groups was more intense. One fish would patrol around the feeding platform, chasing away any fish that came near. Chases covered a longer distance in the asynchronous than in synchronous groups; subordinates would often be chased several times before the aggressor returned to the feeding platform. Overall, the chase rate was higher in the asynchronous than in the synchronous groups (Fig. 4, ANOVA, $F_{1,12} = 25.17$, $P = 0.0003$). Chase rate did not change over time ($F_{6,72} = 1.18$, $P = 0.3300$).

Individual chase rate during a feeding session was correlated with baseline dominance rank in both the synchronous ($n = 28$, $r_s = -0.436$, $P < 0.02$) and the asynchronous ($n = 28$, $r_s = -0.789$, $P < 0.001$) groups (Fig. 5). Surprisingly, dominance was not related to initial body size (Fig. 6, synchronous: total length $r_s = -0.085$, mass r_s

= -0.138, asynchronous: total length $r_s = -0.160$, mass $r_s = -0.138$, $N = 28$ and $P > 0.05$ for all correlations). Dominance rank was significantly concordant over the seven feeding sessions in six of the seven groups for both environments (mean Kendall's τ and range: synchronous 0.595, 0.202 to 0.782, asynchronous 0.593, 0.308 to 0.863).

Variation in fitness

All measures of fitness were independent of the initial body size of individuals. The correlations within both environments between initial mass and initial total length on RO, growth and surplus power were all nonsignificant (P always greater than 0.05).

A total of 3018 eggs were counted during the spawning trials. Of these, 40 eggs were spontaneously released by females. Fifteen of the 40 eggs, could not be assigned to a particular female and thus were excluded from the analysis.

There was no significant difference between treatments in the total number of eggs produced (Fig. 7; synchronous = 1501, asynchronous = 1517). The within-group CV of the total number of eggs per female did not differ significantly between environments (Kruskal-Wallis $\chi^2_1 = 0.147$, $P = 0.3505$). Within a group, the number of eggs produced by the most fecund did not differ significantly between environments (Kruskal-Wallis $\chi^2_1 = 0.200$, $P = 0.3275$).

Similarly there was no difference between the least fecund females (Kruskal-Wallis $\chi^2_1 = 1.135$, $P = 0.1435$). Thus, the variation in fitness as measured by current reproductive output does not appear to differ between environments.

Growth is an indicator of future reproductive output or fitness. The pattern of growth among individuals is similar to that of reproductive output with one exception (Fig. 8). Average growth (Kruskal-Wallis $\chi^2_1 = 0.102$, $P = 0.3745$), within-group CV of growth (Kruskal-Wallis $\chi^2_1 = 0.331$, $P = 0.2825$) and growth rate of the fastest growing fish (Kruskal-Wallis $\chi^2_1 = 0.102$, $P = 0.3745$), did not differ significantly between environments. However, fish with the lowest growth rate lost significantly more body mass in the asynchronous environment compared to the synchronous environment (Kruskal-Wallis $\chi^2_1 = 2.976$, $P = 0.0425$). By the end of the trial, these fish appeared emaciated, and were weak swimmers.

There was no correlation between a fish's allocation of energy into body mass or egg production in either the synchronous groups ($n = 28$, $r = 0.0885$, $P = 0.6542$), the asynchronous groups ($n = 28$, $r = 0.1001$, $P = 0.6124$) or overall (Fig. 9, $n = 56$, $r = 0.0906$, $P = 0.5067$). The distribution of surplus power, the sum of energy allocated to growth and reproduction is shown in figure 10. Average surplus power did not differ between environments (Kruskal-Wallis $\chi^2_1 = 0.102$, $P = 0.3747$). This implies that any

extra energy expenditure from the higher aggression in the asynchronous environment was minimal.

The within-group CV of surplus power was higher in groups fed asynchronously than synchronously (Kruskal-wallis $\chi^2_1 = 2.976$, $P = 0.0423$). Fish with the highest surplus power within a group did not differ significantly between environments (Kruskal-Wallis $\chi^2_1 = 0.004$ $P = 0.475$). However, there was a striking difference between environments for the fish with the lowest surplus power (synchronous, mean = 62.08 j; asynchronous, mean = -262.3 j, Kruskal-Wallis $\chi^2_1 = 3.922$, $P = 0.0238$). Only two fish in the synchronous environment had a negative surplus power compared to 7 in the asynchronous environment. The fish with the lowest surplus power in the asynchronous environment had a surplus power significantly less than zero ($t = 2.35$, $P < 0.05$ one-tailed test). Thus fitness was more variable in the asynchronous than in the synchronous environment.

Correlates of fitness

Aggression and feeding success were positively correlated in the asynchronous environment (Fig. 11, $n = 28$, $r_s = 0.886$, $P = 0.0001$; both ranked within groups). This is in sharp contrast to the synchronous environment where there was no correlation ($n = 28$, $r_s = 0.086$, $P = 0.665$). Fish

displaying an intermediate intensity of aggression appear to have the highest feeding success in the synchronous environment (Fig. 11), but feeding success did not differ significantly for individuals with differing relative aggression (Kruskal-Wallis $\chi^2_3 = 4.74$, $P = 0.192$).

Average feeding success is positively correlated with RO, growth and surplus power in both environments (Fig. 12). Aggression was not significantly correlated with fitness once the effects of feeding rate were statistically removed (Table 1). This is further evidence that the energetic cost of aggression was negligible in this experiment. Thus in the asynchronous environment aggression appears to function as a means for achieving higher feeding success and subsequently fitness. When food arrives synchronously, medaka were not able to increase their feeding success through aggression. However feeding success was still related to fitness.

Discussion

As predicted, the CV of feeding success was higher when food arrived asynchronously compared to when food arrived synchronously. Two factors contributed to this result; both the CV of feeding success during single feeding sessions and the consistency of feeding success across feeding sessions were higher in the asynchronous than in the synchronous

environment. Similar results have been found in other experimental studies. Greater variation of feeding success was found in water striders, Aquarius remigis, (Blanckenhorn 1991a) and zebrafish, Brachydanio rerio, (Grant & Kramer 1992) when food arrived more asynchronously.

The original intent of the synchrony hypothesis was to predict mating systems (Trivers 1972, Emlen & Oring 1977, Wells 1977). The potential for greater resource monopolization under asynchronous conditions is equivalent to what Emlen and Oring (1977) called the environmental potential for polygamy. Support for the synchrony hypothesis from comparative studies is weak. In anurans, Gatz (1981) found no significant pattern between the variation in male mating success and the synchrony of female receptivity. Ryan (1985) reported that the variation in male mating success was actually lower when females became receptive asynchronously, opposite to the prediction of the synchrony hypothesis. In primate troops, Ridley (1986) concluded that one male was able to defend females when they become receptive asynchronously but multi-male troops occurred when females become receptive synchronously. However Altmann (1990) proposed an alternative explanation. Surprisingly, only one experimental study, to date, has shown that variation in mating success is related to the temporal distribution of mates; Grant et al. (in review) found that the CV of male mating success was greater when

females arrive asynchronously than synchronously.

My data support the second prediction of the synchrony hypothesis: animals will use scramble competition when resources are synchronous and interference competition when resources are asynchronous. Not only was the frequency of aggression higher when food arrived asynchronously than synchronously, but there was a positive relationship between the frequency of aggression and feeding success only in the asynchronous environment. These results imply that aggression is an effective method of competing for food in the asynchronous environment but not in the synchronous environment. Similarly, zebrafish increased their intensity of aggression when food arrived more asynchronously (Grant & Kramer 1992), whereas male medaka chased more frequently when competing for females that arrive asynchronously than synchronously (Grant et al. in review).

If aggression has an energetic cost for either the aggressor or the subordinate, the within-group variation of gross benefits may not be equal to the within-group variation of net benefits or fitness. There have been mixed results from previous studies regarding the importance of the cost of aggression. For example, dominant pygmy sunfish, *Elassoma evergladei*, had higher feeding success but did not grow more than subordinates, suggesting a cost of being dominant (Rubenstein 1981). Metcalfe's (1986) reanalysis of Li And Brocksen's (1977) data demonstrated

that subordinate rainbow trout (Onchorhynchus mykiss) are forced to forage in faster current and pay higher energetic costs than dominants. Dominant birds may also have a higher resting metabolic rate, implying a higher energetic cost of aggression, than subordinate birds (Røskaft et al. 1986). However the energetic costs of aggression may be insignificant compared to the risk of injury or lost opportunities (Riechert 1988, Blanckenhorn 1992, Grant et al. in review). The partial correlations for average frequency of aggression and surplus power were not significant in my study. A significant negative correlation would have indicated an energetic cost. The fact that the within-group average surplus power did not differ significantly between environments, despite the frequency of aggression being higher in the asynchronous environment, also indicates that energetic costs of aggression were small.

Previous studies of competition for temporally distributed food resources (Blanckenhorn 1991a, Grant & Kramer 1992) could only measure gross resource monopolization. I demonstrated that variation in growth and surplus power was higher in groups when food arrived asynchronously compared to synchronously. These measures combine the gross benefits of feeding success and gross energetic costs of aggression. Because both growth and surplus power are measures of fitness, selection was more

intense when resources were asynchronous than synchronous. This is the first clear demonstration that the greater variation in feeding success that occurs in asynchronous environments translates to greater variation in fitness, as predicted by the synchrony hypothesis.

The positive correlation between the frequency of aggression and feeding success and between feeding success and fitness in the asynchronous environment implies that food was economically defensible. In the synchronous environment, the frequency of aggression was not associated with either feeding success or fitness. Hence food was not economically defensible in the synchronous environment. However, feeding success was positively correlated with fitness suggesting that good scramble competitors will be selected for in the synchronous environment. This is the first study to show that the distribution of a resource in time can affect the economic defensibility of that resource.

Foraging success is often assumed to be directly related to fitness. For example, the ideal free distribution assumes that feeding rate is equivalent to fitness (Milinski & Parker 1991). This pivotal assumption in behavioural ecology has recently been validated by comparing the fitness of individuals that differ in their choice of prey (Morse & Fritz 1987, Ritchie 1990), relative foraging rate (Burrows & Hughes 1990, Lemon & Barth 1992), and foraging success in a competitive environment

(Blanckenhorn 1991b, Blanckenhorn 1991c). I have extended these observations by showing that there is a linear relationship between feeding success and fitness in two different competitive environments.

An important issue in aquaculture is the fear that selection for rapid growth in food-limited environments may also select for aggressive fish (Doyle & Talbot 1986). If this is the case, greater production may not be achieved because of the energy wasted on aggression. Ruzzante and Doyle (1991) have shown that when medaka compete for unlimited, but spatially clumped food, selection for growth does not select for aggression. They conclude that aggressive fish wasted energy defending surplus food, so selection for increased aggression was prevented. My results suggest that aggression will not necessarily be selected for when food is limited. In the asynchronous environment, aggressive individuals had higher feeding success which led to a higher reproductive output, growth and more surplus power than less aggressive individuals. Hence, selection favoured aggressive individuals in the asynchronous environments. However, when food arrived synchronously, individuals with relatively high chase rates did not have higher feeding success or fitness. This implies that even when food is limited, aggression will only be selected for when the resources are economically defensible.

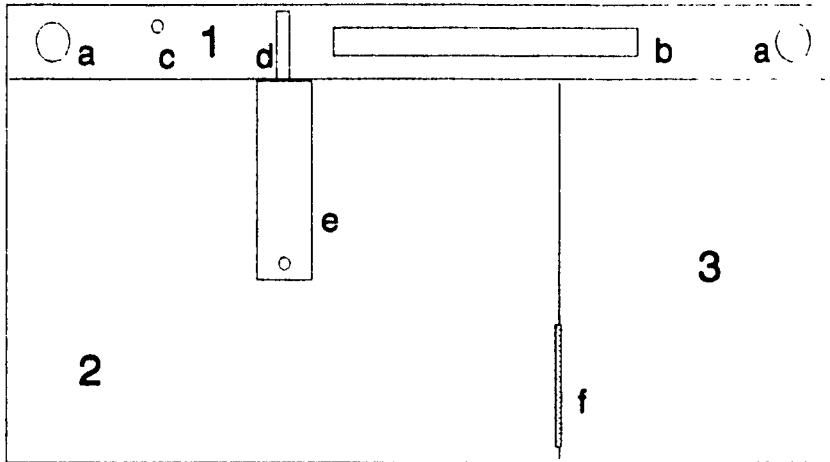
In summary, my experiment has shown that resource monopolization and aggression were higher when food arrived asynchronously than synchronously. Food was economically defensible in the asynchronous but not in the synchronous environment. The correlation between feeding success and fitness combined with the greater variation in feeding success lead to a greater variation in fitness in the asynchronous than in the synchronous environment. This is the first demonstration that the temporal distribution of a food resource has a significant influence on the intensity of selection.

Table 1. Partial correlations of average feeding rate and aggression on reproductive output, growth and surplus power.

Variable	Treatment	Predictor	partial	
			r	P
RO	synchronous	Feeding rate	0.3808	0.0456
		Aggression	-0.0171	0.9324
	asynchronous	Feeding rate	0.3995	0.0352
		Aggression	0.1367	0.4967
Growth	synchronous	Feeding rate	0.4148	0.0282
		Aggression	-0.1038	0.6062
	asynchronous	Feeding rate	0.7630	0.0001
		Aggression	-0.0623	0.7574
Surplus power	synchronous	Feeding rate	0.5380	0.0031
		Aggression	-0.0950	0.6375
	asynchronous	Feeding rate	0.8139	0.0001
		Aggression	0.0719	0.7217

Figure 1. The experimental tank. Compartment 1: a = undergravel filter stalk with air stone, b = heater, c = water input tube for feeding system, d = water and food output tube for feeding system. Compartment 2, "The feeding chamber": e = feeding platform, g = gravel. Compartment 3, "The spawning chamber": f = sliding door.

Top view



Front view

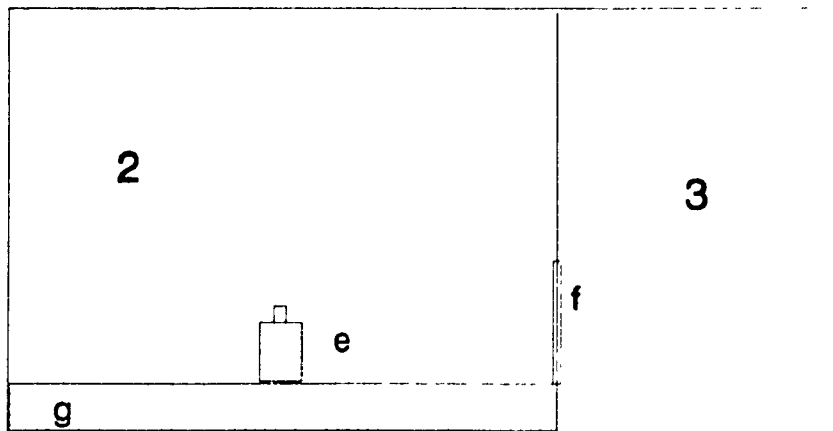


Figure 2. Monopolization of food as measured by the Coefficient of Variation of feeding success per feeding session over the 14-day experiment. Means (symbols) \pm 1 SE (lines) are plotted. Circles = asynchronous, squares = synchronous.

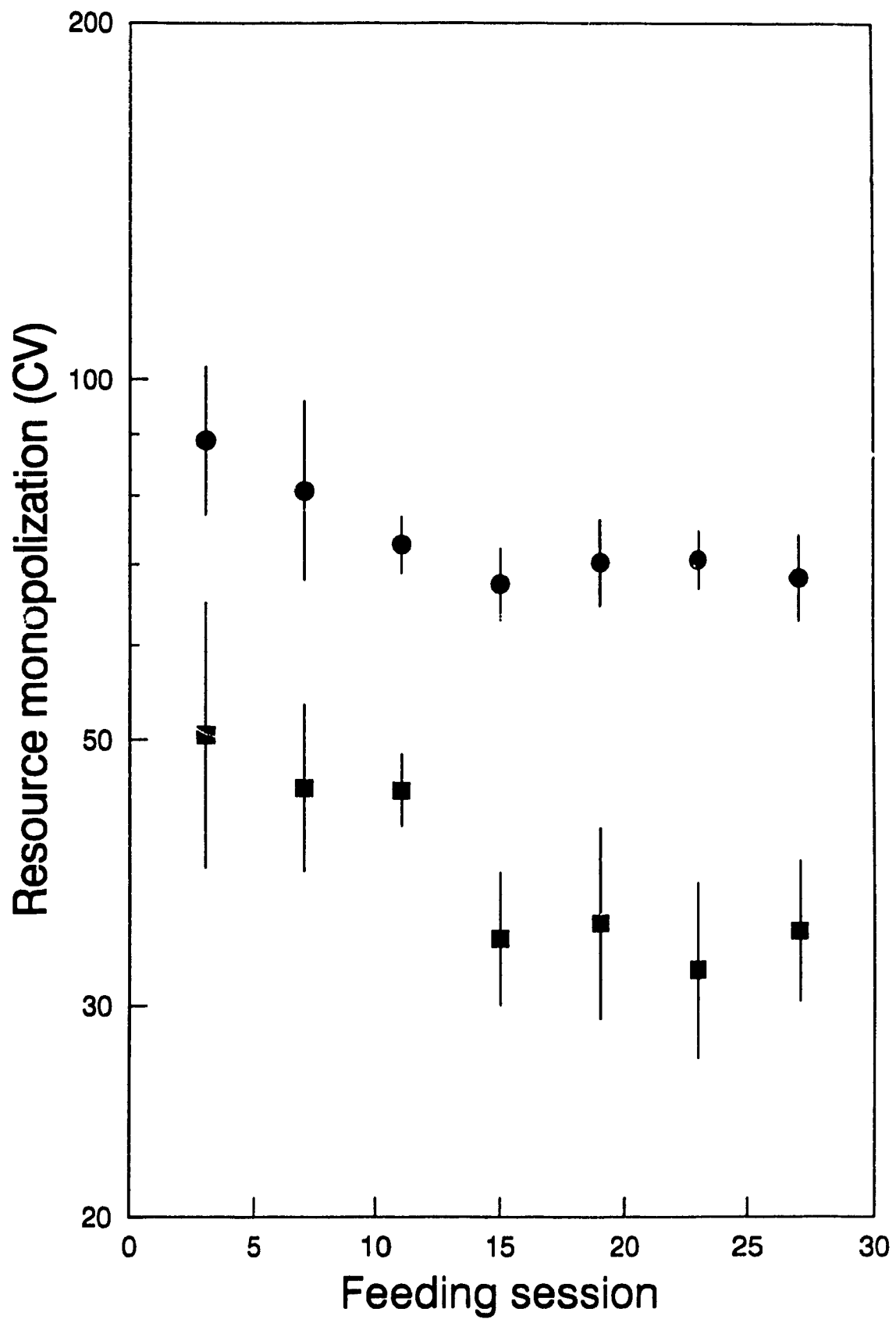


Figure 3. Total feeding success as measured by the sum of ingested shrimp on the seven videotaped feeding sessions. Fish were ranked by feeding success (1 = most successful). Bars are means \pm 1 SE. Open bars are from synchronous, hatched bars are from asynchronous. Dotted bar indicates expected total feeding success (multinomial distribution) of ranked fish.

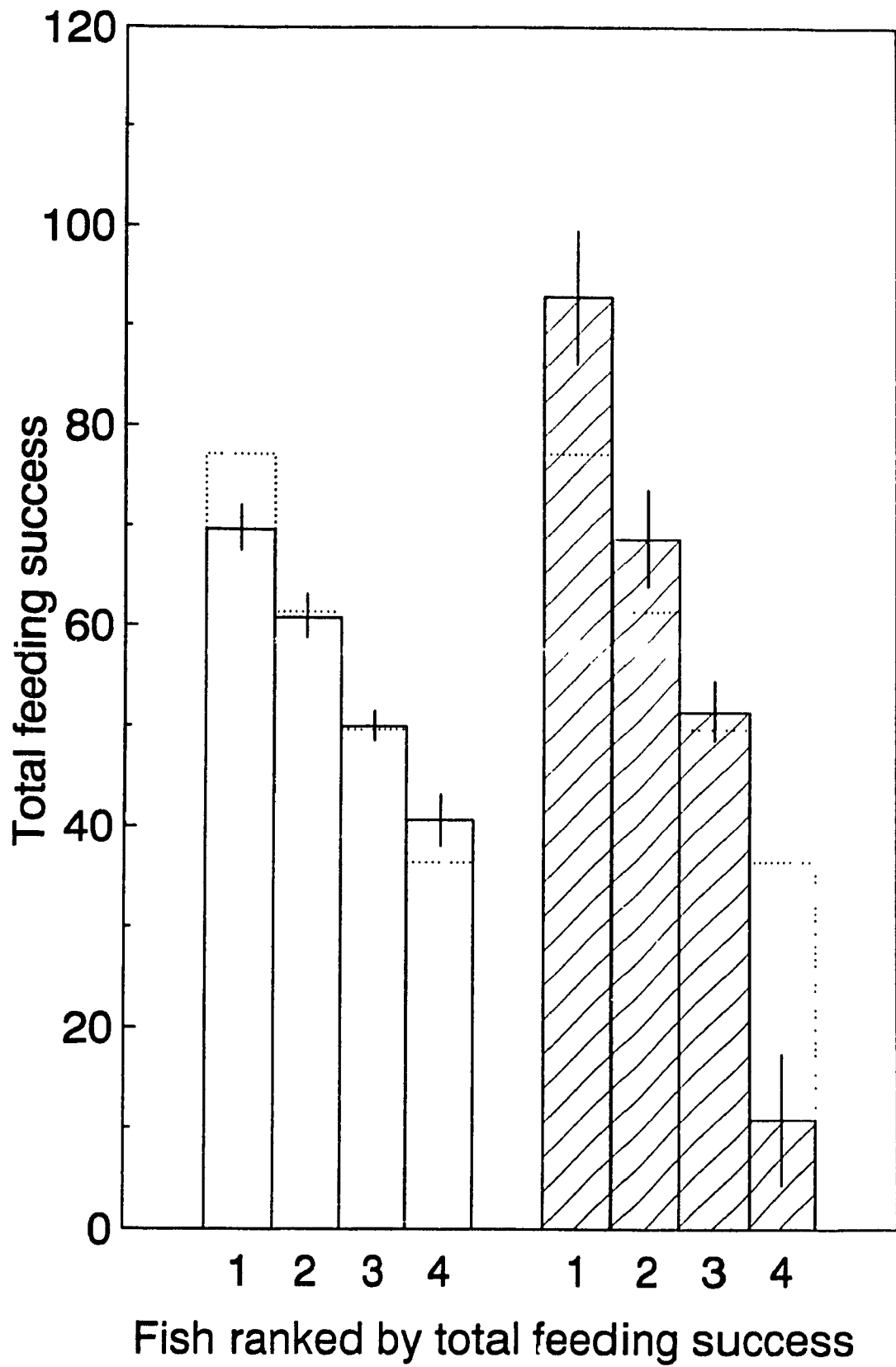


Figure 4. Frequency of aggression as measured by chases per min. Means (symbols) \pm 1 SE (lines) are plotted. Circles = asynchronous, squares = synchronous.

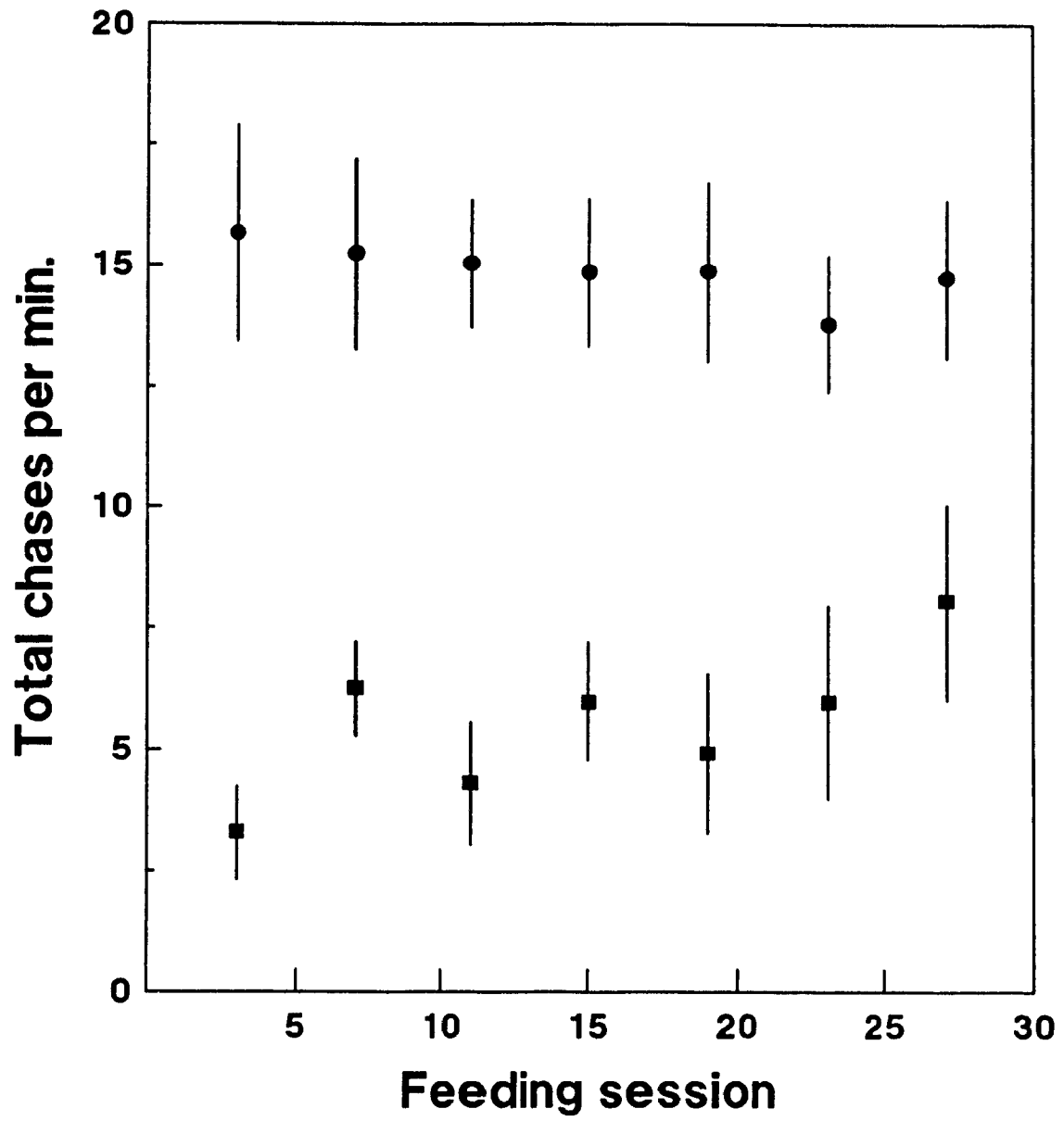


Figure 5. Average dominance rank prior to seven feeding sessions (1 = most dominant) in relation to an individual's ranking in average chase rate (1 = most aggressive). Bars are means \pm 1 SE. Open bars are from synchronous environment, hatched bars are from asynchronous environment.

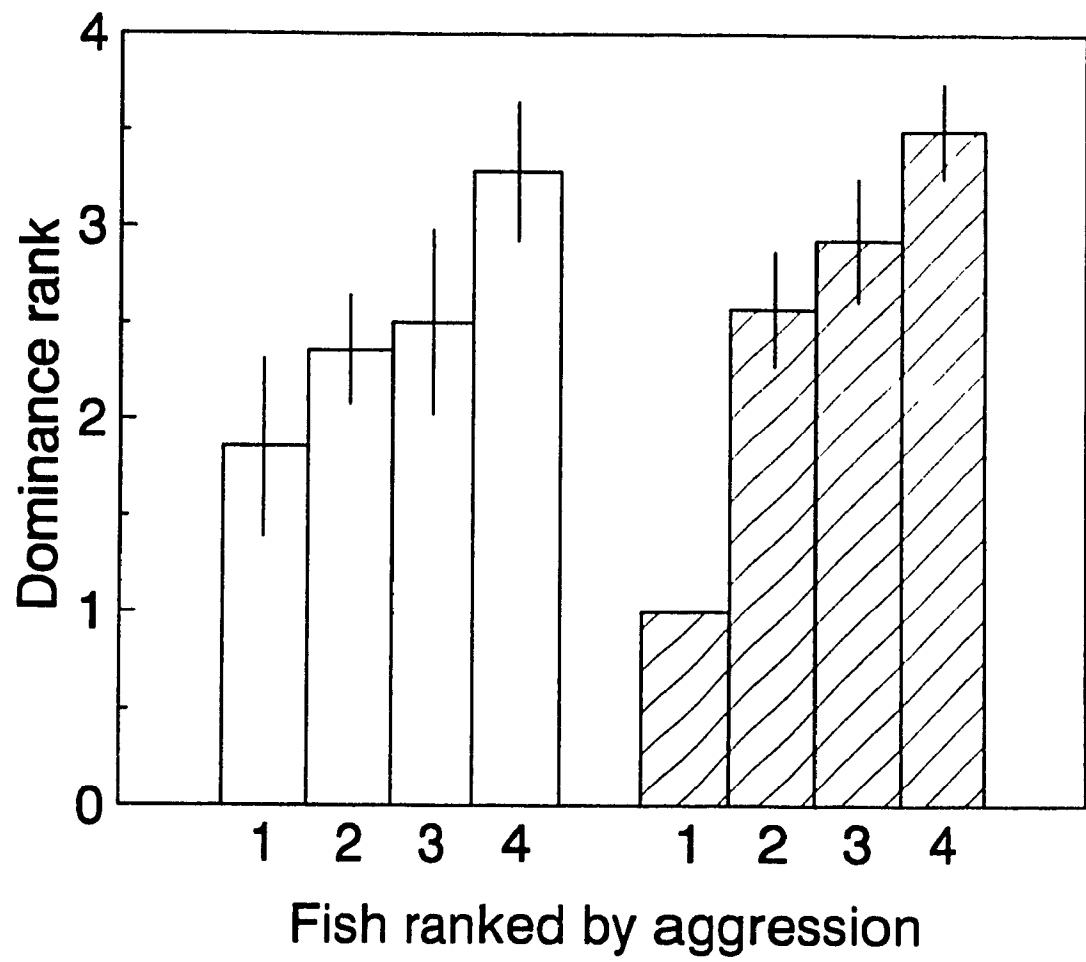


Figure 6. Body size for individuals ranked by average dominance rank (1 = most dominant). Bars are means \pm 1 SE. Open bars are from synchronous, hatched bars are from asynchronous.

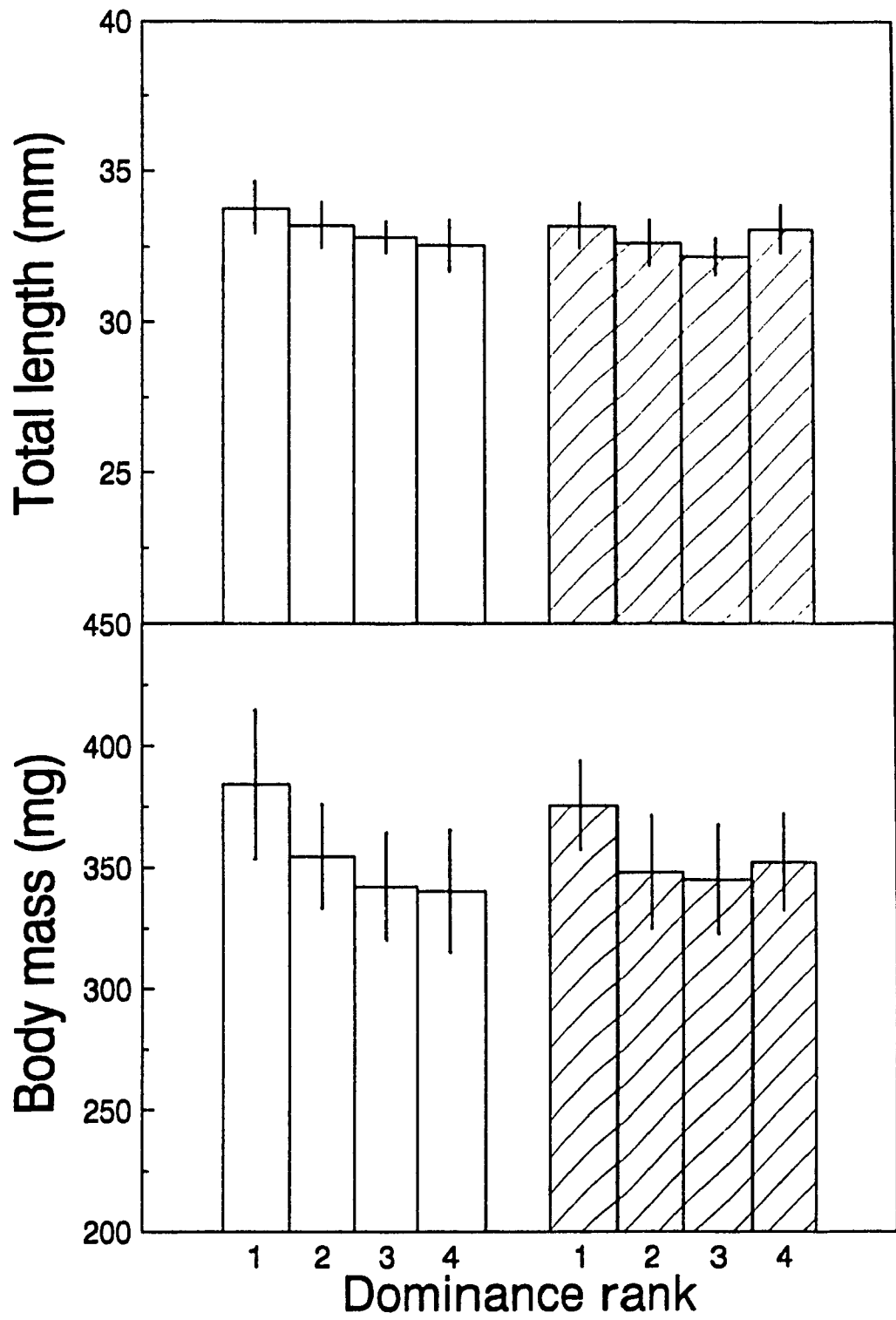


Figure 7. Distribution of reproductive output (number of eggs) within-groups. Fish were ranked by number of eggs within groups (1 = fish with the most eggs). Bars are means \pm 1 SE. Open bars are from synchronous, hatched bars are from asynchronous.

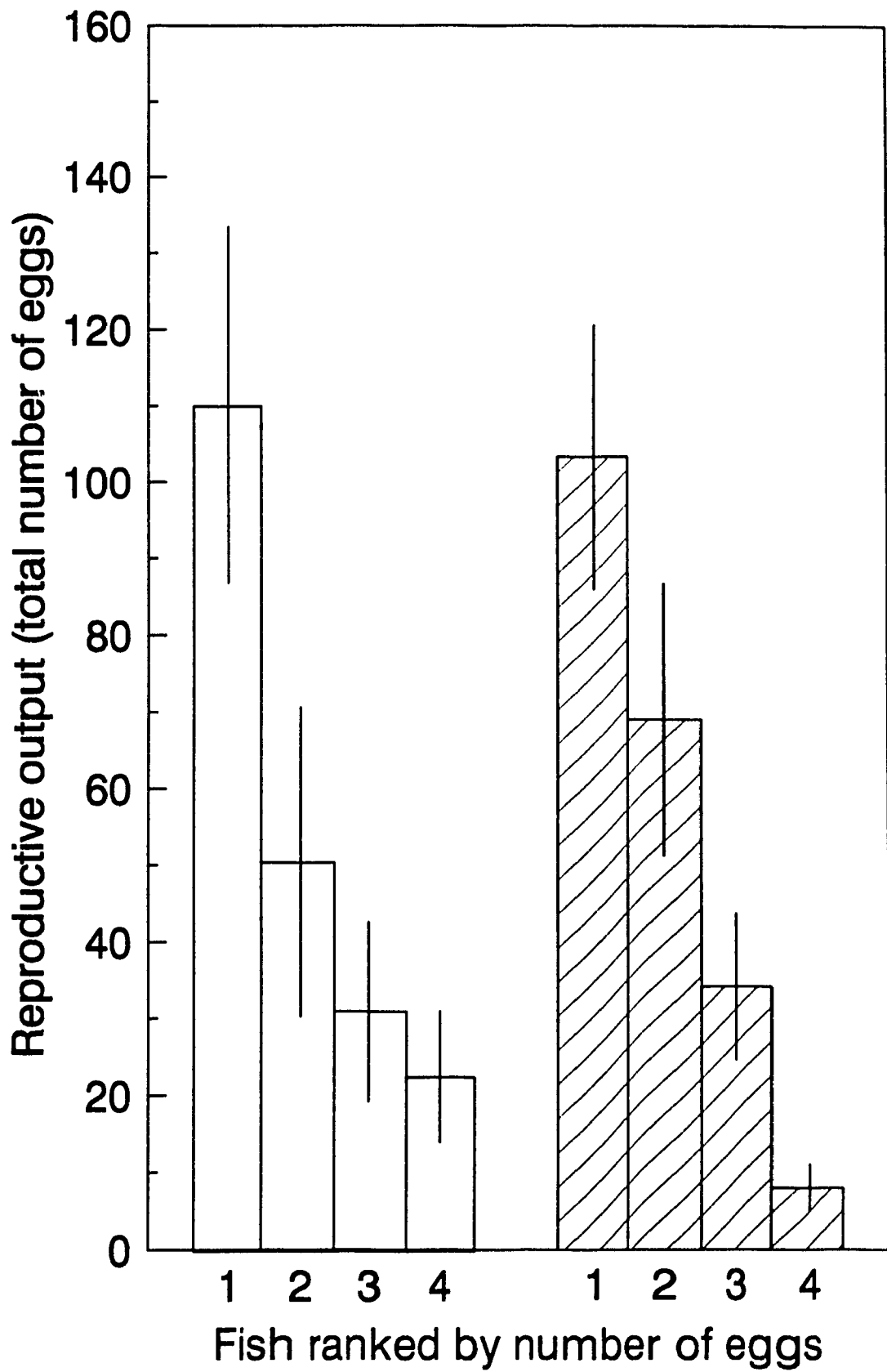


Figure 8. Distribution of growth within-groups. Fish were ranked by growth within groups (1 = fish with the greatest growth). Bars are means \pm 1 SE. Open bars are from synchronous, hatched bars are from asynchronous.

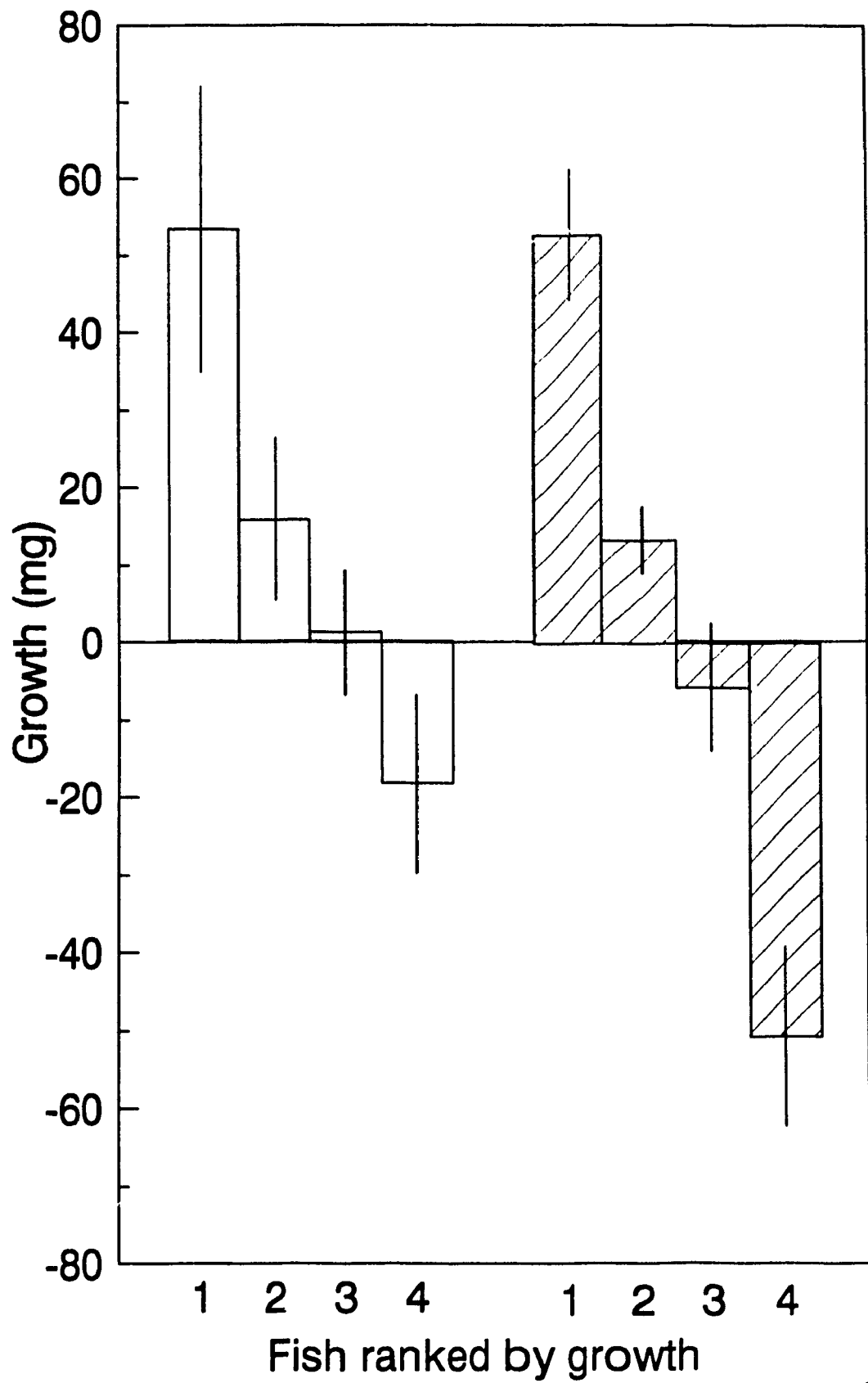


Figure 9. Energy allocated to reproduction or growth.
Squares are from synchronous, circle are from asynchronous.
Dotted line indicates zero surplus power.

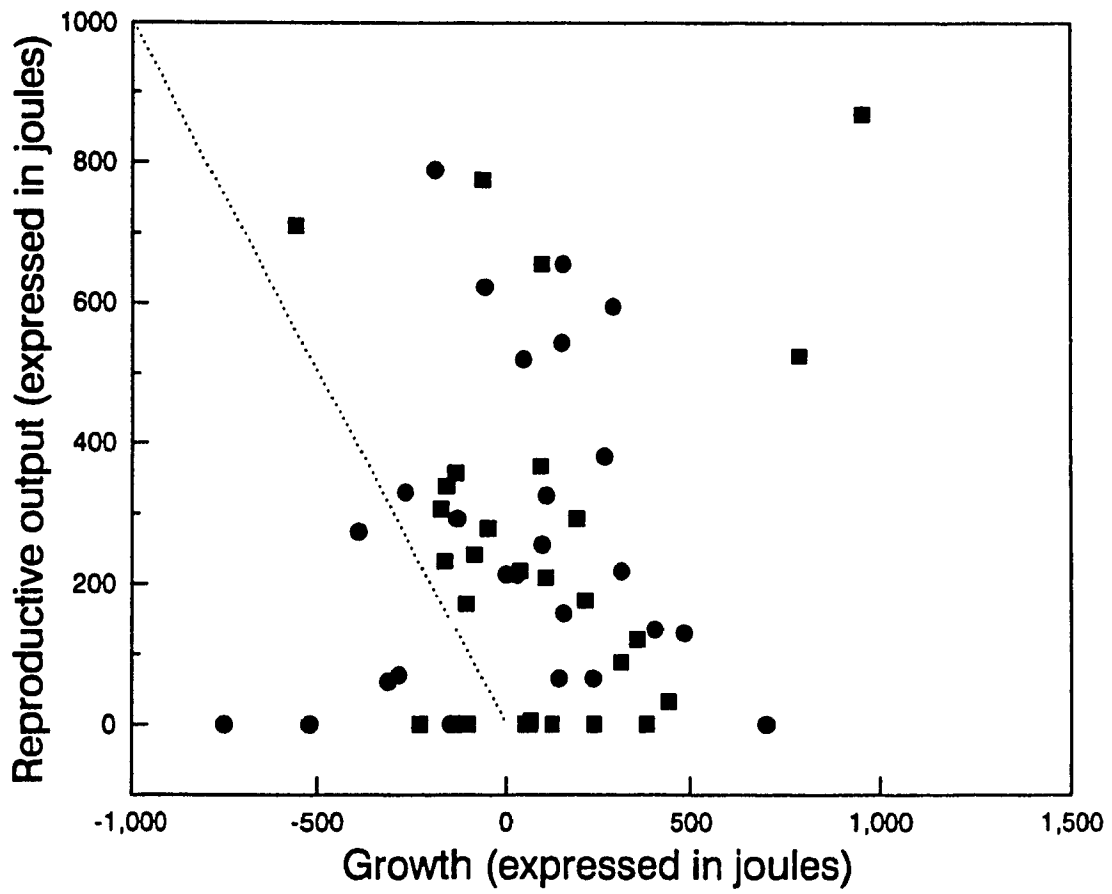


Figure 10. Distribution of surplus power within-groups. Fish ranked by surplus power within groups (1 = fish with the most surplus power). Bars are means \pm 1 SE. Open bars are from synchronous, hatched bars are from asynchronous.

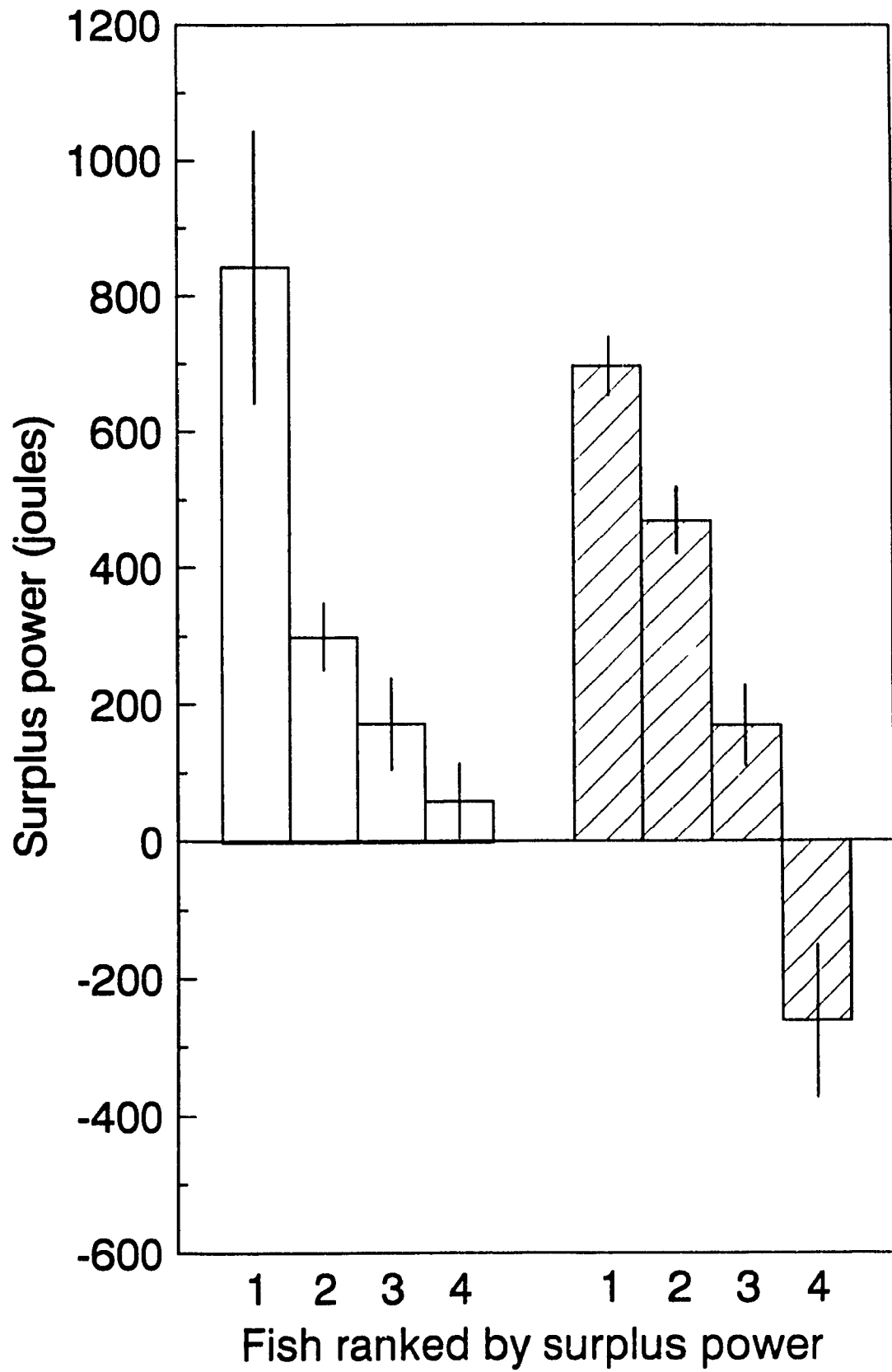


Figure 11. Feeding success by ranked average aggression (4 = most aggressive). Bars are means \pm 1 SE. Open bars are from synchronous, hatched bars are from asynchronous.

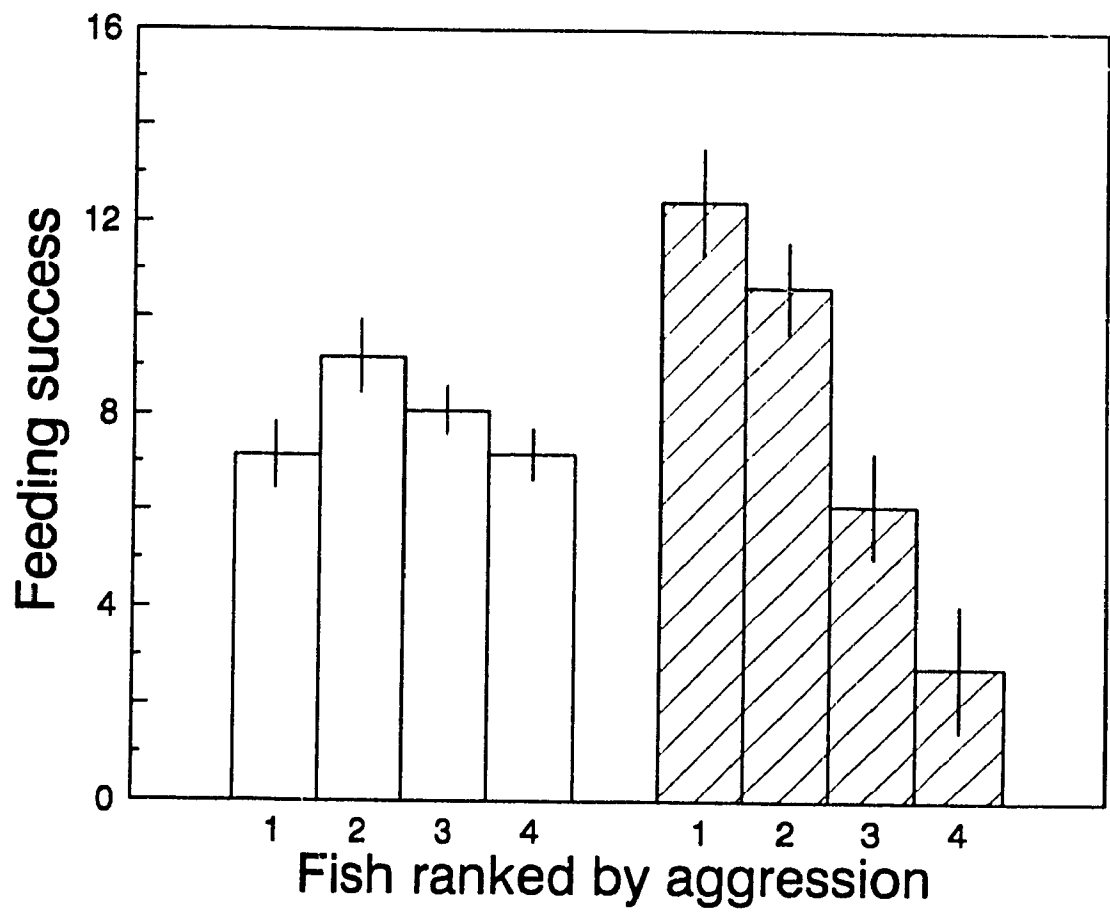
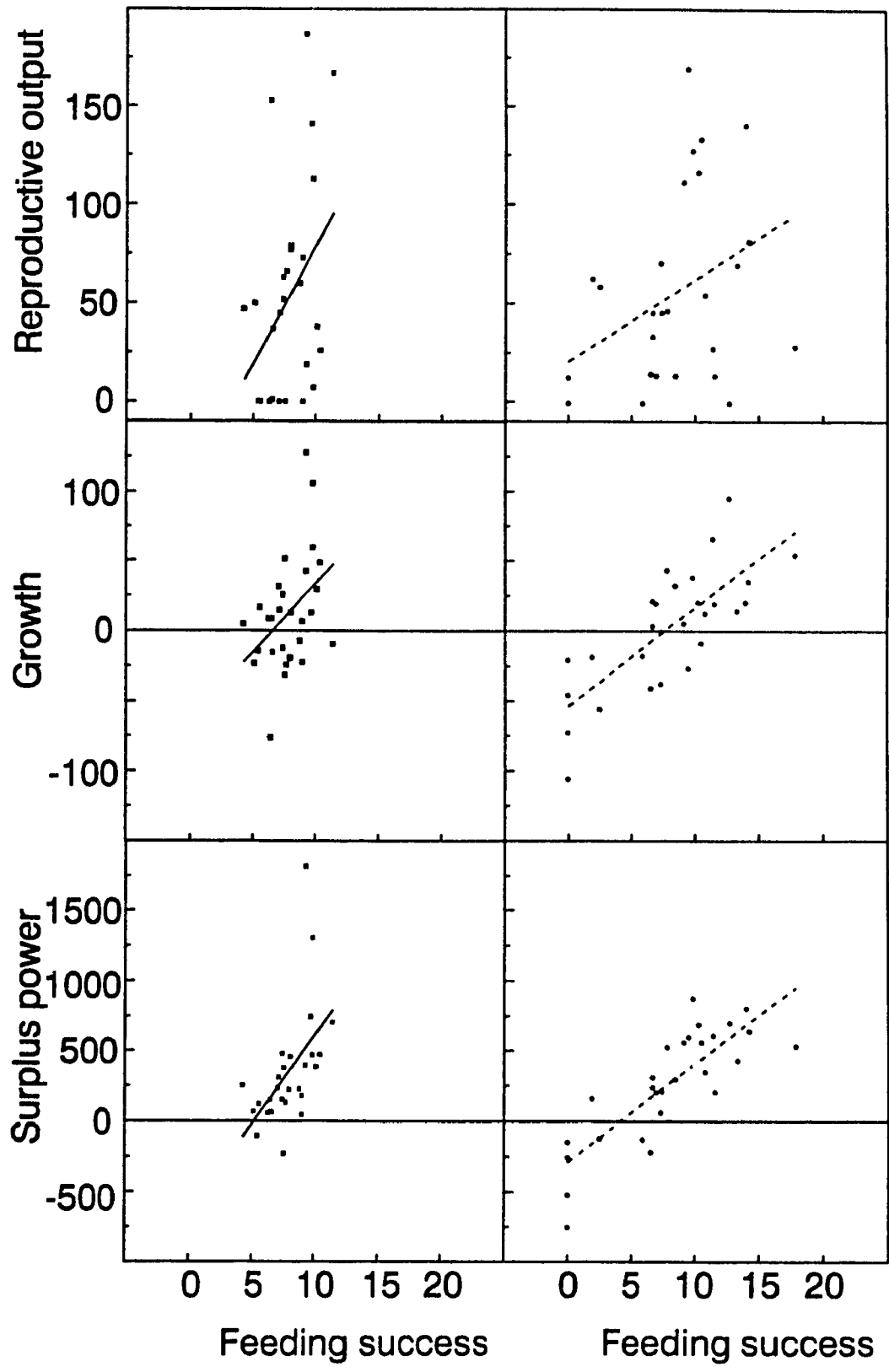


Figure 12. The relationship between average feeding success and reproductive output, growth, and surplus power. Lines indicate the least square regression line. Circles = asynchronous, squares = synchronous.



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