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ARTICLES

The foraging and antipredator behaviour of growth-enhanced transgenic Atlantic salmon

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Growth rate has been established as a key parameter influencing foraging decisions involving the risk of predation. Through genetic manipulation, transgenic salmon bred to contain and transmit a growth hormone transgene are able to achieve growth rates significantly greater than those of unmanipulated salmon. Using such growth-enhanced transgenic Atlantic salmon, we directly tested the hypothesis that relative growth rates should be correlated with willingness to risk exposure to a predator. We used size-matched transgenic and control salmon in two experiments where these fish could either feed in safety, or in the presence of the predator. The first experiment constrained the predator behind a Plexiglas partition (no risk of mortality), the second required the fish to feed in the same compartment as the predator (a finite risk of mortality). During these experiments, transgenic salmon had rates of consumption that were approximately five times that of the control fish and rates of movement approximately double that of controls. Transgenic salmon also spent significantly more time feeding in the presence of the predator, and consumed absolutely more food at that location. When there was a real risk of mortality, control fish almost completely avoided the dangerous location. Transgenic fish continued to feed at this location, but at a reduced level. These data demonstrate that the growth enhancement associated with the transgenic manipulation increases the level of risk these fish are willing to incur while foraging. If the genetic manipulation necessary to increase growth rates is achievable through evolutionary change, these experiments suggest that growth rates of Atlantic salmon may be optimized by the risk of predation.

In studying animal design, it is generally assumed that phenotypes have been shaped by many generations of selection. Within their design constraints, these organisms should therefore be well adapted to their environment. However, this assumption is inappropriate when studying transgenic organisms. Within a single generation, the characteristics of the organism have been modified with no opportunity for selection and adaptation to their environment. Comparison of transgenic organisms to those without the transgene provide the unique opportunity to explore animal design by directly quantifying the costs associated with a modified design. One character that has been manipulated with transgenic fish is growth rate. While this has obvious economic benefits, it is also of evolutionary interest (see Sibly et al. 1985). The more rapidly fish grow, the fewer their predators, and the greater the range of potential prey (Werner & Gilliam 1984). They may also reach sexual maturity earlier (Alm 1959). Why then have small fish not been selected to maximize their growth rates?

One possible explanation is that fish must make decisions that do not simply maximize their feeding rate but also include other ecologically important parameters. Perhaps the most studied parameter is the impact that risk of predation has upon foraging decisions. As a consequence, there has been considerable interest in developing models to investigate the role of risk. These include analytical methods (Werner & Gilliam 1984; Gilliam & Fraser 1987; Ludwig & Rowe 1990; Abrams 1991; Leonardsson 1991; Houston et al. 1993) and dynamic

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Table 1. Size of predators used in experiments 1 and 2

Fish	Length (cm)	Weight (g)
1	28.8	317.0
2	24.9	213.1
3	28.3	335.6

state variable techniques (McNamara & Houston 1986; Mangel & Clark 1986, 1988). Despite their differences in methodology, all of these models have predicted a solution generally similar to that originally proposed by Werner & Gilliam (1984): populations of animals should occupy habitats that minimize the ratio of mortality rate (μ) to growth rate (g). Gilliam & Fraser (1987) have provided experimental support for a modified form of this model.

From this theoretical work, it is clear that there are two factors important in determining whether an animal should risk exposure to a predator: parameters that affect mortality rates (i.e. the probability of being killed by a predator over a discrete period) and growth rates (e.g. the life history characteristics of the animal, particularly the future fitness benefits associated with food). Experimental work has demonstrated that reduced vulnerability to predators, such as increased size (Johnsson 1993) or the presence of antipredator morphology (McLean & Godin 1989; Abrahams 1995), results in animals being more likely to feed in the presence of a predator. The benefits of food are more difficult to determine. Starved or parasitized animals are relatively more willing to risk exposure to a predator (Dill & Fraser 1984; Godin & Sproul 1988). In addition, the absolute amount of food and its distribution are also important considerations affecting decisions involving the risk of predation (Cerri & Fraser 1983; Fraser & Huntingford 1986; Gilliam & Fraser 1987; Holbrook & Schmitt 1988; Abrahams & Dill 1989), although the results vary depending upon the design of the experiment, species and sex.

To understand better the influence of growth rates on decisions involving the risk of predation, we tested the hypothesis that a transgenic manipulation that increases growth rate should cause these individuals to risk greater exposure to predators in order to increase their feeding rate.

METHODS

The fish used in these experiments were produced at the Aqua Bounty hatchery in Prince Edward Island, Canada. This facility is government inspected with respect to the required containment measures for working with genetically modified fish. All transgenic fish used in all of the crosses and all control fish were Atlantic salmon, *Salmo salar*, originally derived from the St John River, New Brunswick, stock. The gene construct was comprised of an antifreeze protein gene promoter from the Ocean Pout, *Macrozoarces americanus*, spliced to the growth hormone gene from Chinook salmon, *Oncorhynchus tshawytscha* (Hew et al. 1995). Approximately 10^6 copies of the gene construct were injected through the micropyle of normal fertilized, but nonactivated, eggs in 1989 according to the method of Shears et al. (1992). One of the fast-growing males (F_0) was crossed with a female in the autumn of 1991. A fast-growing F_1 female was crossed with a normal male in the autumn of 1994 and again in the autumn of 1996. The F_2 fish from both these crosses produced offspring with a bimodal size distribution with approximately equal numbers of fish in the upper and lower mode, suggestive of a gene insert on a single chromosome. There was approximately a 10% overlap between the two modes when the upper mode had achieved a mean size of 5 g, and 0% overlap when the upper mode had a mean weight of 10 g. We used polymerase chain

Table 2. Mean±SD sizes of fish used in experiment 1 and their tag colours

Group	Type	Length (cm)	Weight (g)	Tag colour
1	Transgene	8.90±0.28	5.77±0.40	White
1	Control	8.05±0.36	5.70±0.56	Blue
2	Transgene	9.03±0.18	5.95±0.33	Blue
2	Control	8.13±0.15	5.53±0.20	White
3	Transgene	9.05±0.27	5.57±0.31	Blue
3	Control	7.85±0.18	5.18±0.43	White
4	Transgenic	9.45±0.23	7.35±0.23	White
4	Control	8.13±0.08	5.53±0.29	Blue
5	Transgenic	9.25±0.11	6.65±0.38	White
5	Control	8.30±0.25	5.78±0.33	Blue
6	Transgenic	9.35±0.21	6.65±0.36	Blue
6	Control	8.20±0.31	5.65±0.71	White
7	Transgenic	9.63±0.15	7.43±0.25	Blue
7	Control	8.40±0.21	6.30±0.67	White
8	Transgenic	9.43±0.19	7.50±0.86	Blue
8	Control	8.27±0.23	6.00±0.42	White
9	Transgenic	9.43±0.19	6.85±0.42	White
9	Control	8.10±0.19	5.35±0.32	Blue

Table 3. Mean±SD sizes of fish used in experiment 2 and their tag colours

Group	Type	Length (cm)	Weight (g)	Tag colour
10	Transgenic	9.45±0.28	6.60±0.62	No tag
10	Control	9.30±0.14	8.30±0.63	No tag
11	Transgenic	9.38±0.52	6.65±0.95	No tag
11	Control	9.15±0.15	8.30±0.57	No tag
12	Transgenic	9.40±0.35	6.53±0.60	No tag
12	Control	8.85±0.29	7.55±0.85	No tag
13	Transgenic	9.95±0.23	7.88±0.94	Yellow
13	Control	8.10±0.10	5.45±0.22	Blue
14	Transgenic	9.05±0.64	6.27±1.14	White
14	Control	8.65±0.17	6.80±0.25	No tag
15	Transgenic	9.77±0.25	7.63±0.84	Red
15	Control	8.03±0.11	5.80±0.24	No tag

reactions (PCR) to confirm that the two modes were distinguished by the presence or absence of the transgene. The transgenic fish used in the present study were from the upper modal group of the 1996 spawning. Fish used as controls were obtained from eggs and milt from the same river stock but from nontransgenic parents. The eggs of both transgenic and control fish were fertilized on 5 November 1996, but in order to arrive at comparable body weights for these experiments, the transgenic eggs were incubated in cooler water. This procedure delayed the time of first feeding by 4 weeks. Both groups of fish were raised in 300-litre fibreglass tanks at 13–14°C and a natural photoperiod. They were provided with excess rations fed three times per day.

We identified transgenic and control fish using differently coloured tags, which were made of acetate and coloured using nontoxic acrylic paint. We randomly assigned tag colour for each group in each experiment. Each tag consisted of two coloured squares of acetate welded to a fine piece of monofilament thread (invisible sewing thread). To attach each tag, we anaesthetized the fish with tertiary amyl alcohol. We then inserted a sterile 27-gauge needle through the dorsal muscle, anterior of the dorsal fin, passed the monofilament line through the needle, and welded a second coloured tag to the other end of the line, securing the tag. This procedure allowed us identify fish independent of their orientation to the camera.

After tagging, the fish were placed in a general holding tank for a minimum of 2 days where they were provided a crumble feed (EWOS Vextra Start Size 2) exclusively via an automated feeder (see Abrahams 1989). This provided the fish time to recover from the tagging procedure and anaesthesia, and also allowed them to learn to use the feeders that would be used during these experiments.

To begin each experiment, we randomly selected four transgenic fish and four control individuals as subjects. These fish were placed in rectangular, grey fibreglass flow tanks (220 × 31.5 × 31 cm) with a glass front and a coarse gravel substrate. Each tank was illuminated by a 56-cm long flourescent light (General Electric Bright Stik) mounted 32 cm above the surface of the tank. Illumination of these tanks approximated the natural photoperiod.

Experiment 1: Proximity to a Predator

To conduct these experiments, we divided the apparatus into two equal halves by a transparent Plexiglas partition. To one side we added a large rainbow trout, *Oncorhynchus mykiss* (Table 1); the other side contained the eight experimental fish. All fish were placed in the apparatus approximately 16 h prior to beginning experiments.

Experiments began at 0700 hours the following day. Two feeders provided 0.2 g of crumble feed each to the test fish uniformly over 20 min. One feeder was situated 60 cm from the transparent partition and was designated the safe feeder. The other feeder was situated 5 cm from the partition and was considered the dangerous feeder. Data were obtained by starting both feeders

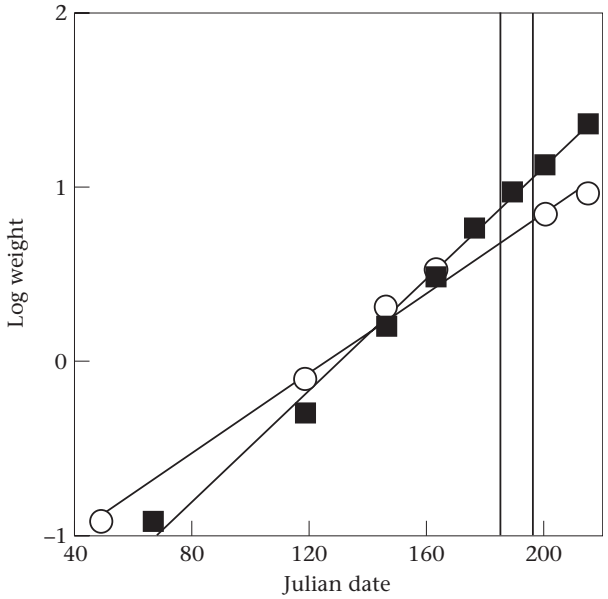

Figure 1. Growth rates of the control (○) and transgenic (■) fish used in these experiments. Regression lines through the log-transformed data have an R^2 value of 0.993 for both the transgenic and control fish. Experiments were conducted from Julian days 185 to 196.

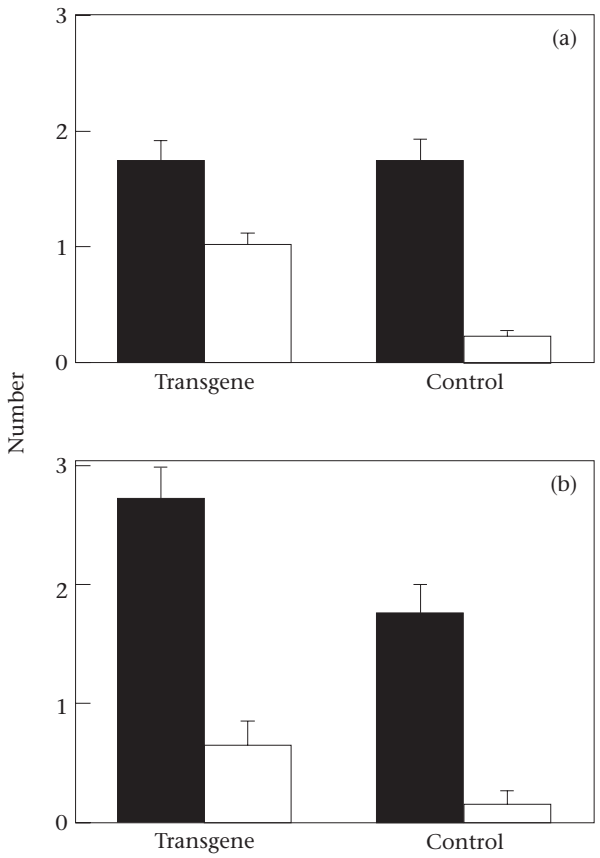

Figure 2. The influence of predators on the foraging behaviour of transgenic and control fish. The mean+SE number of fish feeding at either the dangerous (□) or safe (■) location when the predator was (a) behind a transparent Plexiglas partition, and (b) in direct contact with the fish feeding at the dangerous location.

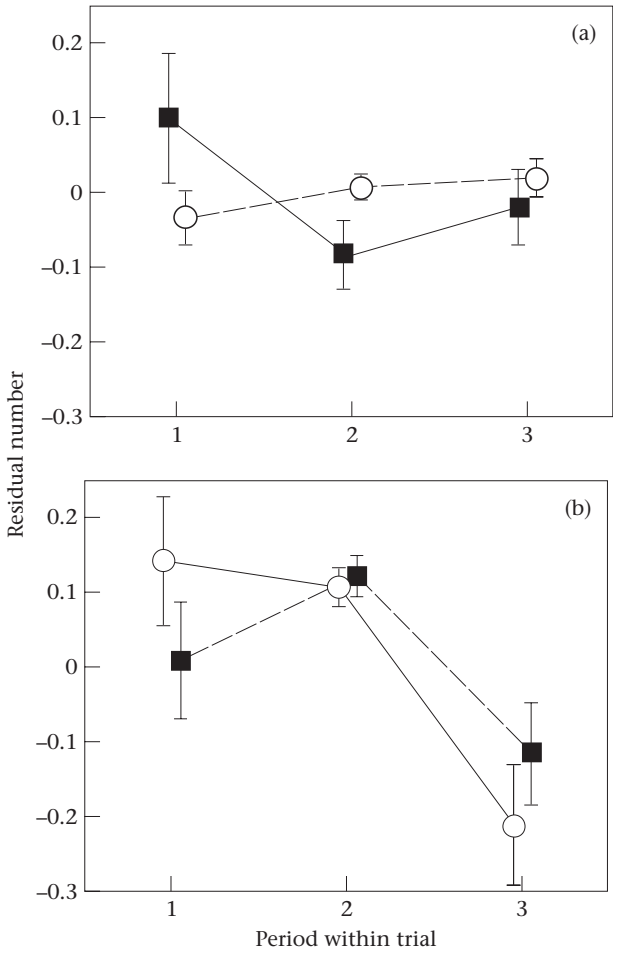

Figure 3. The residual number ±SE of control (○) and transgenic (■) fish using the (a) dangerous and (b) safe feeders when the predator was behind a Plexiglas partition.

simultaneously, and recording the spatial distribution of the fish every 30 s for 20 min. This allowed us to determine the relative use of the dangerous and safe locations by the control and transgenic fish. In addition, the entire experiment was videotaped using Hi-8 video cameras to determine the amount of food consumed, and the detailed behaviour of the fish.

We conducted a second trial the same day, beginning at 1500 hours. Upon completion of the second trial, we reversed the location of the predator, and conducted a second set of trials the following day. After completion of the second days' trials, we removed all experimental fish from the apparatus and recorded their wet weight and fork lengths. We again randomly determined predator position, and placed another group of fish in the apparatus, with observations to begin the following day. Three replicate sets of the apparatus were used, allowing three experiments to be conducted simultaneously. This allowed more groups to be used during the limited time that both the transgenic and control groups were of similar size. A total of nine different groups of fish were used for these experiments (Table 2).

To assess activity levels of transgenic and control fish, we randomly selected a transgenic and control fish during the first and last 5 min of each 20-min videotaped trial and traced their movements onto acetate film. We then determined the total distance travelled from these tracings using a Jandel graphics tablet. By obtaining two measures from each trial, a total of eight measures were provided on distance moved by transgenic and control fish for each group.

Experiment 2: Direct Access to the Predator

To distinguish whether the mode of predator presentation affected the behaviour of these fish, we conducted a second set of experiments that required the fish to have direct contact with the predator in order to gain access to the food at the dangerous feeder. This experiment was similar to that described above except that the apparatus was divided by a coarse-mesh partition (4-cm stretch mesh size) rather than clear Plexiglas. The mesh was of a size that allowed the small salmon to use both halves of the apparatus, but restricted the large predator to one side. The dangerous feeder was now located 3 cm within the predator side of the apparatus, requiring fish to feed in direct contact with the predator. For this experiment, six different groups of size-matched fish were used (Table 3).

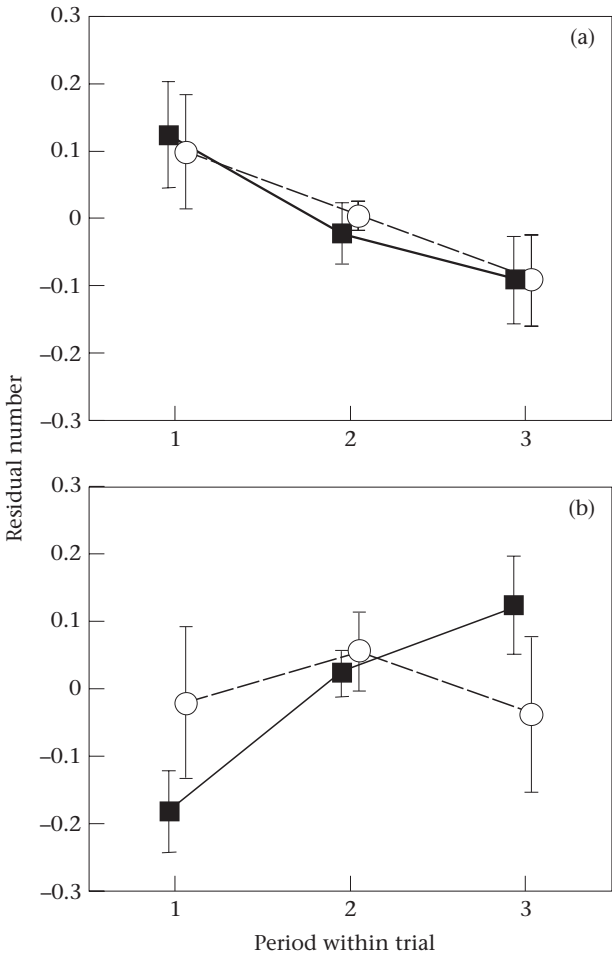

Figure 4. The residual number ±SE of control (○) and transgenic (■) fish using the (a) dangerous and (b) safe feeders when they had direct contact with the predator.

All statistical analyses used the GLM procedure of SPSS.

Ethical Note

The tagging procedure used in these experiments did not impede the swimming ability or cause distress to these fish. We removed all tags from the fish after they were used in these experiments. Because we used a very fine needle and thread for these tags, the size of the puncture wound was very small and all fish were completely healed within 2 days. No infections were observed due to our sterile procedures and the relatively sterile water used by this facility.

The design of these experiments meant that encounters between predators and prey were not forced. In the first experiment, there was no direct contact between predator and prey, and visual contact was limited to four 20-min trials. In the second experiment, which involved direct contact, prey initiated and terminated contact with the predator. Furthermore, the proximity of the dangerous feeder to the mesh partition, and the ease with which the prey could pass through the partition, made the probability of capture very low. We also stacked the odds in favour of the prey by using hatchery-reared fish as predators that had no experience capturing live prey. To minimize stress to our fish in these experiments, we used a coarse gravel substrate that allowed fish that did not risk exposure to the predator to also employ crypsis as an additional antipredator strategy.

We also minimized energetic stress to our fish by using experiments that lasted only 2 days. Predators were fed maintenance rations for the duration of these experiments.

RESULTS

The growth rates of the transgenic and control fish are illustrated in Fig. 1. As these data demonstrate, the transgenic fish had a significantly greater rate of growth (1.53%/day) than did the control fish (1.05%/day) under identical temperature conditions and throughout the weight interval of 1–10 g. Due to this considerable disparity in growth rate, there was a limited time when experiments could be conducted using transgenic and control fish of approximately similar size. As illustrated in Tables 2 and 3, transgenic and control fish were matched by weight, but transgenic fish tended to be longer.

In addition to variation in patterns of growth, the transgenic fish were also distinct from the control fish in several other traits. The transgenic fish were more silvery and had paler parr marks, allowing them to be distinguished from control fish (for more details see Stevens et al. 1999). They were also more active than control fish (see below) and fed more readily during experiments. Average participation rates by transgenic fish were approximately 80%, whereas for control fish they were usually less than 50%. Qualitatively, transgenic fish appeared to be less affected by handling than control fish.

Habitat Selection

The spatial distribution of both the transgenic and control fish are summarized in Fig. 2. Both transgenic and control fish avoided feeding in the presence of the predator, but the magnitude of this response depended upon fish type. Significantly more transgenic fish fed in the presence of the predator than did control fish (ANCOVA: $F_{1,33}$=6.90, P=0.013; Fig. 2). While there was a small difference in size between the control and transgenic fish, this did not account for a significant proportion of the variation (ANCOVA: $F_{1,33}$=2.88, P=0.099). These data demonstrate that the transgenic fish were more willing than the control fish to feed in the presence of a predator, and that this variation in behaviour could not be accounted for by any variation in size between the control and transgenic fish.

The method by which the predator was presented had a significant influence on the number of transgenic fish that fed at the dangerous feeder (ANOVA: $F_{1,13}$=21.2, P<0.001). When the fish had direct contact with the predator (experiment 2), transgenic fish reduced their use of the dangerous feeder and increased their use of the safe feeder (Fig. 2). Control fish did not show this sensitivity in their response; there was no difference observed in

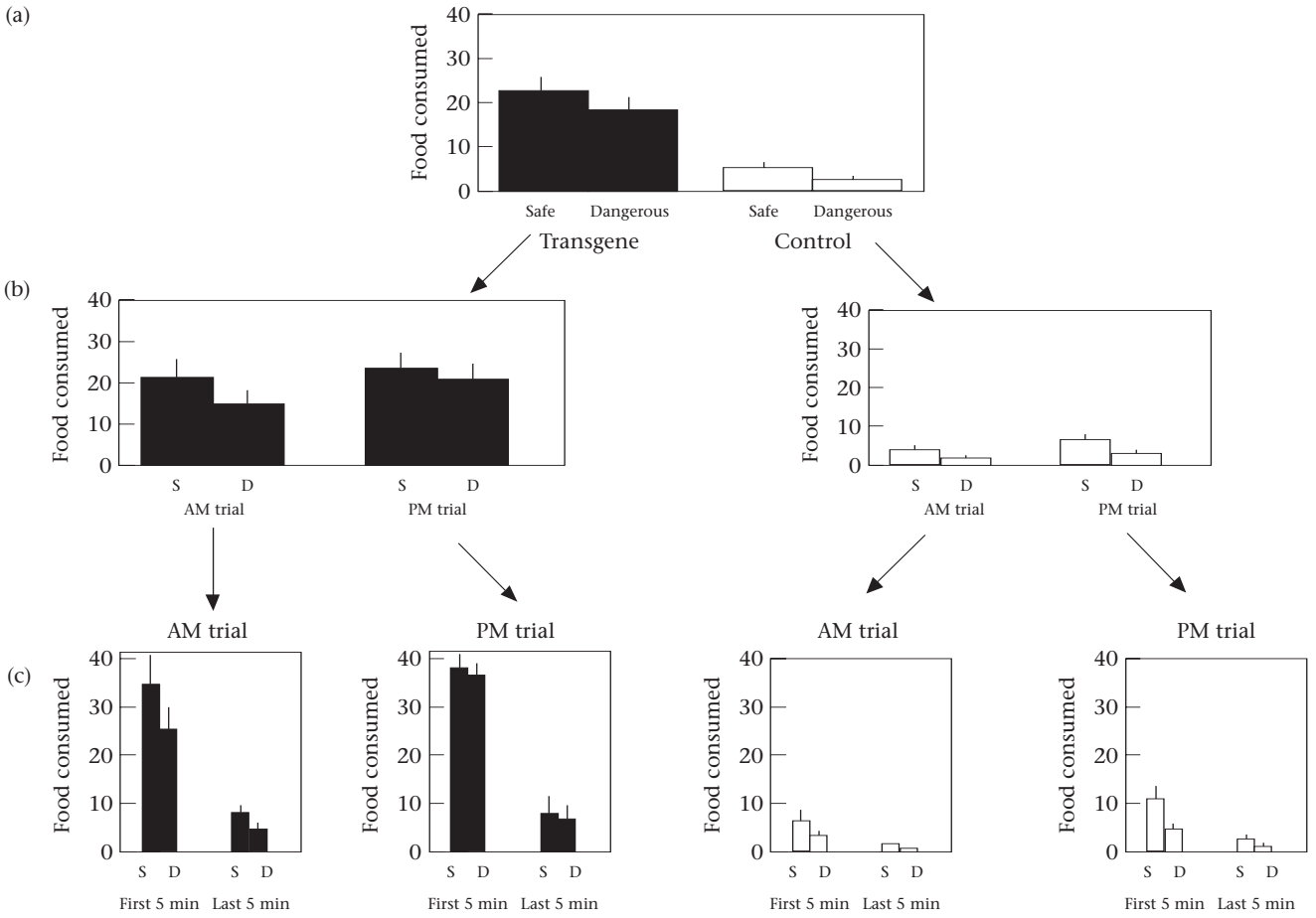

Figure 5. The average+SE amount of food consumed by transgenic (■) and control (□) fish at the safe and dangerous feeding sites in experiment 1 (a) when the predator was behind a transparent Plexiglas partition (all trials combined), (b) during the morning (AM) and afternoon (PM) trials, (c) during the first and last 5 min within a trial.

their use of the dangerous feeder between the two experiments (ANOVA: $F_{1,13}$=1.1, P=0.31; Fig. 2). When these fish did have direct access to the predator, none was captured.

To determine whether transgenic and control fish varied their behaviour over time, we divided each trial into three equal time periods. Within each time period, we determined the number of transgenic and control fish at the safe and dangerous sites, and subtracted this value from the mean for the entire trial. Positive values indicated above average use of a feeder, and negative values were below average. This analysis demonstrated significant variation in behaviour over time (repeated measures ANOVA: $F_{2,32}$=7.35, P=0.002). Furthermore, there was a significant interaction between the level of risk and change in behaviour through time ($F_{2,32}$=4.25, P=0.023). At the safe feeder, both control and transgenic fish reduced their use of the safe feeder towards the end of the trial (Fig. 3). The pattern at the dangerous feeder was not obvious and appeared to vary between the transgenic and control fish (Fig. 3). However, there was no statistically significant interaction between fish type and variation in behaviour through time ($F_{2,32}$=3.09, P=0.06).

When the salmon had direct access to the predator, the temporal pattern of behaviour also changed (Fig. 4), but this change was not statistically significant ($F_{2,20}$=0.704, P=0.51). In addition, there were no significant interactions between time and the type of fish ($F_{2,20}$=2.62, P=0.10), or between time and the safe and dangerous feeder ($F_{2,20}$=1.9, P=0.18).

Consumption Rates

In both experiments and at all time levels there were clear differences in the consumption rates of transgenic and control fish (Figs 5, 6); transgenic fish always consumed approximately five times as much food as the control fish. Proximity to the predator had a significant influence upon the amount of food consumed in both experiments (Table 4). Beyond this scalar difference, there were general patterns that were common to both experiments 1 and 2. Fish type, proximity to the predator, time of day and time within a trial all had a significant influence on consumption rates (Table 4). The latter two effects reflected an overall pattern for increasing consumption rates in afternoon experiments, and a decrease

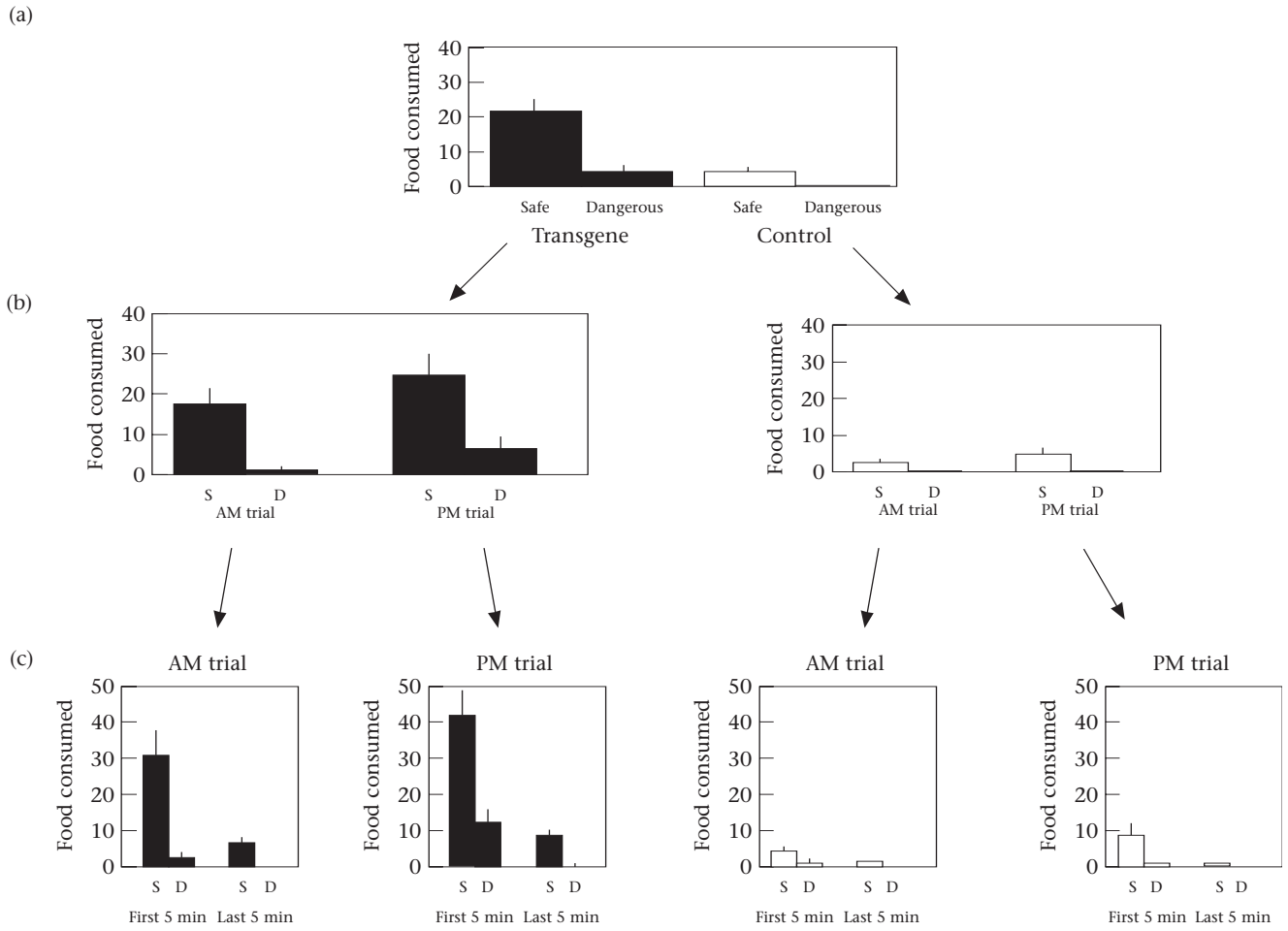

Figure 6. The average+SE amount of food consumed by transgenic (■) and control (□) fish at the safe and dangerous feeding sites in experiment 2 (a) when these fish had direct access to the predator (all trials combined), (b) during the morning (AM) and afternoon (PM) trials, (c) during the first and last 5 min within trials.

in consumption rates at later times within a trial (Figs 5, 6). A significant interaction existed between fish type and time within trial (Table 4), although the general pattern for the change in consumption rates was common to both transgenic and control fish (Figs 5c, 6c). There was also a significant interaction between time of day and time within trial on consumption rates. This was due to the reduced change in feeding rates within a trial for the morning trials compared with the afternoon trials (Figs 5c, 6c). In both experiments there was also a significant three-way interaction between predator, side and trial (Table 4) and this may have been due to some variation in the behaviour of the predators that we used.

There were significant interactions between predator and fish type, and predator and time within trial unique to experiment 2 (Table 4). The first interaction may have been due to the near complete avoidance by the control fish of the predator in this experiment, combined with an overall reduction in their feeding rate (compare Figs 5a, 6a). The interaction between predator and time reflects the general increase in the amount of food consumed at the dangerous location in the afternoon trial relative to the morning trial (Fig. 6b).

Speed of Movement

As with consumption rates, there was a significant difference between the speed of movement of transgenic and control fish (Table 5, Fig. 7a). Transgenic fish had an average speed of 328 cm/min, compared with 96 cm/min for control fish. Unlike feeding rates, there was no statistically significant influence of time of day or time within a trial on these data (Table 5). These data demonstrate that transgenic fish maintained a speed advantage at all times within a given day (Fig. 7b) and at all times within a given trial (Fig. 7c).

DISCUSSION

Our experiments demonstrated that fish that had been genetically modified to have accelerated growth rates were significantly more willing to risk exposure to a

Table 4. Summary of statistically significant parameters and their interactions that influenced the amount of food consumed in experiment 1 and 2*

Parameter	*F*	*P*
Experiment 1 (predator confined)		
Predator	8.6	0.042
Fish type	44.1	0.003
Time within day	51.7	0.002
Time within trial	68.0	0.001
Fish type×time within day	25.8	0.007
Time within day×time within trial	46.8	0.002
Predator×side×trial	7.9	0.048
Experiment 2 (direct access to predator)		
Predator	23.2	0.005
Fish type	14.5	0.013
Time within day	15.3	0.011
Time within trial	19.7	0.007
Predator×fish type	10.4	0.023
Predator×time within trial	14.0	0.013
Fish type×time within trial	9.6	0.027
Time within day×time within trial	11.1	0.021
Predator×side×trial	13.7	0.014

*Repeated measures ANOVA with five main effects (predator, fish type, tank side used for predator presentation, time within day, and time within trial). All numerator *df* were 1. Error *df* for experiment 1 were 4 (due to some missing data) and 5 for experiment 2.

Table 5. Analysis of the parameters that may influence the rates of movement in Atlantic salmon*

Source	*df*	*F*	*P*
Fish type	1	13.70	0.002
Day	1	0.32	0.580
Time within day	1	0.20	0.660
Time within trial	1	1.67	0.220

*Repeated measures ANOVA. All interactions were nonsignificant. Error *df* were 14.

predator in order to gain access to food. These results are consistent with theoretical expectations about how animals should integrate the risk of predation into their foraging decisions (e.g. Werner & Gilliam 1984). Not only did this manipulation alter behaviour, but it also significantly increased feeding rate and the average speed of movement. These data suggest that linked hormonal control of growth rate and behaviour may be the proximate mechanism that optimizes growth rates of fish.

An unanticipated result was the ability of transgenic fish to reduce their exposure to predators in response to increases in the magnitude of risk. As a consequence, their more active behaviour may not necessarily translate directly into an increased mortality rate when they are directly confronted with predators. Indeed, it is possible that the elevated growth rates enjoyed by transgenic fish under ideal conditions may be diminished significantly under more natural condition as has been observed for young cotton rats, *Sigmodon hispidus*, subjected to elevated thyroid hormone levels (T_4; Derting 1989). In Derting's study, the growth rates of manipulated cotton rats exceeded those of unmanipulated controls when the rats were provided food ad libitum. However, when food was restricted, the growth rate of the control group exceeded that of the manipulated group. Thus T_4 elevated the metabolic rate of these animals. Under restricted feeding conditions, this increased cost resulted in reduced growth relative to the unmanipulated control. However, with unrestricted food, the increased activity levels allowed them to grow at rates exceeding that of the control group.

Previous experiments by Jönsson et al. (1996) have demonstrated that rainbow trout treated with growth hormone are more willing to risk exposure to a predator than unmanipulated fish. Johnsson et al. (1996) demonstrated a similar result for brown trout, *Salmo trutta*. These authors have interpreted their results to indicate that levels of growth hormone represent a balance between the positive effects of growth and the increased mortality associated with changes in antipredator behaviour. Within a hatchery, where there are no predators, they argue that this balance will be altered (Johnsson et al. 1996). Our results our consistent with their observations.

Key to the interpretation of these results is that accelerated growth rates will be accompanied by increased mortality rates. Due to time constraints we were not able to address this issue experimentally. However, under natural conditions, we believe there are two mechanisms that would elevate the mortality rate of transgenic salmon in relation to their wild counterparts. First, salmon containing this transgene lose their parr marks more rapidly than their wild counterparts (Stevens et al. 1998). Parr marks are known to provide a camouflage advantage to juvenile salmonids on a gravel substrate (Donnelly & Dill 1984). If this morphological change is not accompanied by a habitat shift from streams to oceans, then these transgenic salmon should have a higher probability of being detected and killed by visually hunting predators. Furthermore, our data, and those of Jönsson et al. (1996), have indicated that an additional response to elevated growth hormone levels is an increase in activity level. Werner & Anholt (1993) have theorized that elevated movement by prey will increase their encounter rate with food, but also with predators. These factors, in combination with the greater willingness by transgenic salmon to risk exposure to predators, does suggest that they will suffer higher mortality rates under natural conditions.

A major ecological concern associated with transgenic fish is their potential to escape captivity and become an invading species (Kapusckinski & Hallerman 1990, 1991; Kareiva et al. 1996). These fish could damage wild stocks of Atlantic salmon either by directly displacing them, or by interbreeding with wild fish, producing individuals that are less able to survive in the wild. At this point, it is difficult to assess the likelihood of either outcome. Proponents of the transgenic technology propose using reproductively incapable fish (female triploids) to reduce the risk of swamping of wild gene pools. The escape of transgenic brood stock into stream habitats might pose a

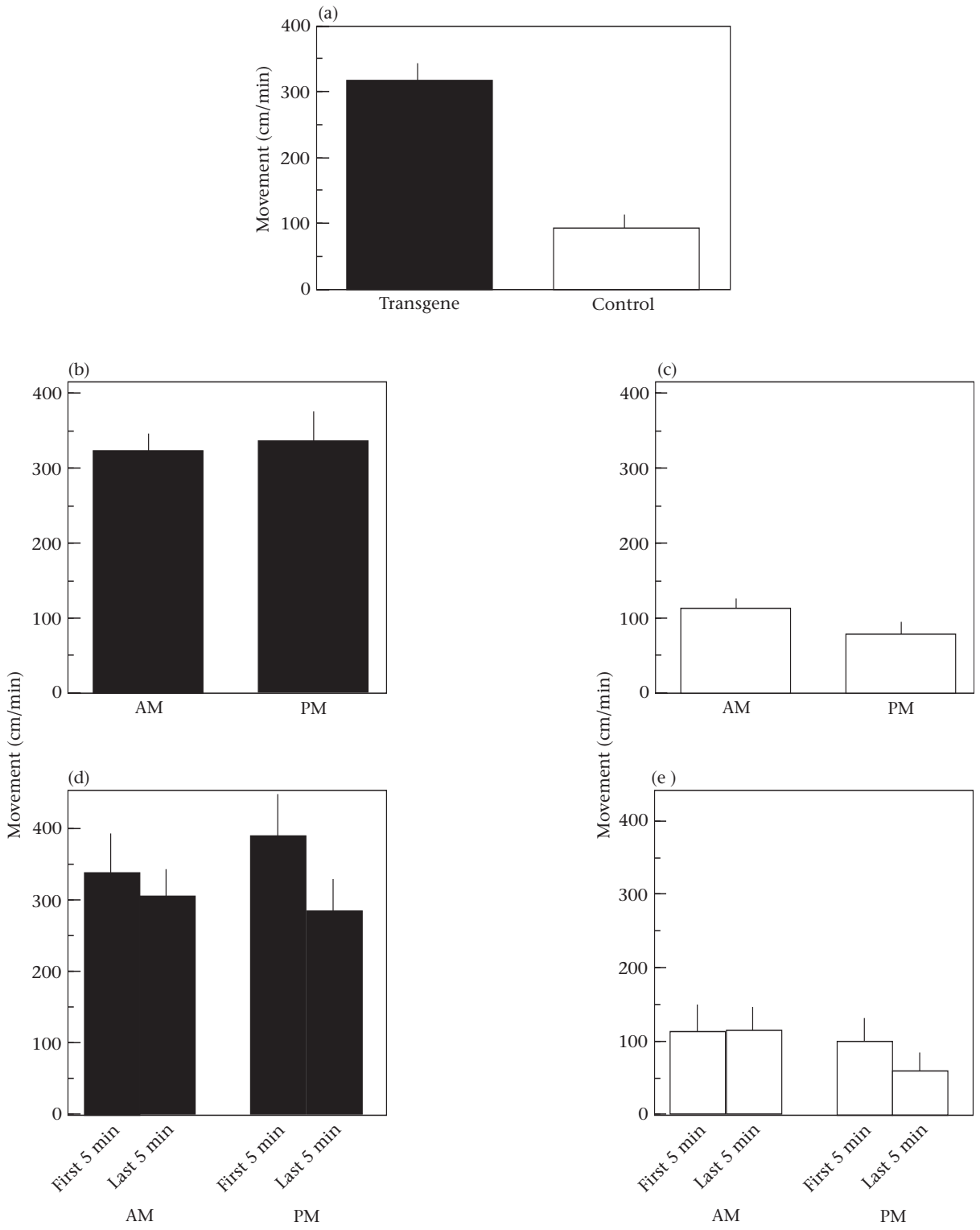

Figure 7. Average+SE travel speed for transgenic (■) and control (□) fish in (a) all trials combined, (b, c) morning and afternoon trials and (d, e) the first and last 5 min in morning (AM) and afternoon (PM) trials.

problem if the growth-enhanced fish were able to dominate wild fish in securing territory or food. However, if hormone levels are selected to maximize net benefits (Ketterson & Nolan 1992), then the costs associated with accelerated growth more than offset the benefits. Our data suggest that these costs may be associated with the enhanced appetite and increased activity levels of transgenic fish, increasing their susceptibility to predators. Indeed, Stevens et al. (1998) have demonstrated that these transgenic salmon have a 50–70% higher routine

and basal metabolic rate than control fish. This may render them less able to withstand extended periods of food deprivation.

However, at this point this is speculation. It is not yet possible to predict whether any species is capable of successfully invading an ecosystem (Kareiva et al. 1996). Yet we believe that further research into the ecological impacts of transgenic salmon is crucial as they present us with a paradox. While their escape may have a negative impact on wild stocks, their commercial development may also benefit these populations by relieving some of the economic pressures confronting the dwindling wild stocks.

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