INTERACTIONS BETWEEN GROWTH, SEX, REPRODUCTION, AND ACTIVITY LEVELS IN CONTROL AND FAST-GROWING STRAINS OF NILE TILAPIA, *OREOCHROMIS NILOTICUS*

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ABSTRACT

This study examined the relationship between growth, behavioral activity, and sexual maturation in control strains of Nile tilapia, *Oreochromis niloticus* (Family Cichlidae) and in strains resulting from a project devoted to the Genetic Improvement of Farmed Tilapias (GIFT). Locomotor and agonistic activity of fish groups was video recorded each month of the three-month study period. Under laboratory conditions, the fast-growing GIFT fish performed less locomotor and agonistic activity than the slow-growing control fish. Mirror image stimulation tests performed on individual males supported the finding that controls are more aggressive than GIFT fish. Nesting behavior, which is often the first indication of sexual maturity, was observed only in males; also the slow-growing control fish became sexually mature sooner, and at a smaller size than the fast-growing GIFT fish. These results are thus fully compatible with the hypothesis that oxygen supply limits the growth of fish, that calm behavior allows reallocation of oxygen to somatic growth, and that, in contrast, high activity levels reduce growth and lead to earlier maturation, at smaller sizes.

INTRODUCTION

One important production trait of farmed fish is its size at first sexual maturation. Fish strains that possess a high growth rate and reach harvestable size before attaining sexual maturation are sought by fish culturists because sexual maturation and spawning complicate production operations and/or affect product quality. This is especially important for the tilapias (mainly *Oreochromis* and *Tilapia*, Fam. Cichlidae), fish of African origin, which is now farmed for local and export markets in over 80 countries (e.g., Philippines, Taiwan, Israel, and the United States). When tilapia are stocked in an unpopulated pond or another aquaculture facility, the fish often shift towards a more altricial life style, characterized by a shorter period of somatic growth, an earlier onset of reproductive maturity, and more numerous, smaller eggs (Fryer and Iles 1972; Noakes and Balon 1982). The fish become “stunted,” in that they are smaller than other adults of the same species. These stunted individuals are unsuitable for the market, thus causing problems in the fish industry. This provides the overall background for the work presented here.

Wild vs. hatchery-reared fish

Growth rate comparisons have been made between wild and hatchery-reared fish. Vincent (1960), and Flick and Webster (1964) observed in the brook trout, *Salvelinus fontinalis*, that under hatchery conditions, farmed fish grew faster than wild stocks. Einum and Fleming (1997), and Fleming and Einum (1997) also observed, under hatchery conditions, faster growth in farmed Atlantic salmon, *Salmo salar*, than in wild stock. Even under natural conditions, wild stock had a lower growth rate than farmed fish (Einum and Fleming 1997). Furthermore, Davis and Fenderson (1971) observed in Atlantic salmon that, even though hatchery and wild parr were matched for size when introduced to a divided outdoor stream aquarium, hatchery parr were on average larger in size than wild parr as the study progressed. Overall, hatchery-reared fish seem to have a growth advantage over wild fish stocks.

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Wild and hatchery-reared fish differ not only in growth rates, but also in their behavioral activity. Bachman (1984) observed in the brown trout (*Salmo trutta*) that hatchery-reared fish fed less than wild fish. A similar feeding pattern was observed in Atlantic salmon (Fenderson *et al.* 1968; Sosiak *et al.* 1979). Sosiak (1978) also observed in Atlantic salmon that hatchery parr were less shelter-oriented and more mobile than wild parr, and exhibited higher frequencies of agonistic behaviors. Norman (1987), in contrast, found Atlantic salmon fry of the hatchery stocks to be less aggressive.

Holm and Fernö (1978) went a step further in their study, by examining the connection between aggressive activity and growth rate. They observed that aggressive Atlantic salmon parr grew less rapidly, while parr with the most rapid growth performed aggressive actions less frequently (Holm and Fernö 1978). These results imply a negative relationship between aggressive activity and growth. Furthermore, Robinson and Doyle (1990) found a negative correlation between aggression and growth in the tilapia hybrid, *Oreochromis mossambicus* x *O. hornorum*. Unfortunately, there is little information on the relationship between activity and growth in farmed-reared and wild fish stocks. Thus, more research is needed to examine these relationships to see to what extent growth differences between farmed-reared and wild fish can be attributed to differences in locomotor and/or aggressive activity levels of fish stocks.

**Sexual dimorphism**

As information has accumulated on growth rates of various fish species, it has become apparent that either a) the males and females of a given species grow at the same rate and have similar maximum sizes (e.g., herrings); b) the females have faster growth rates and reach larger size than the males (e.g., codfishes), or c) the males have faster growth rates and become larger than the females (e.g., cichlids) (Fryer and Iles 1972). The sex-related growth differences in cichlids, including Nile tilapia, are well established (van Someren and Whitehead 1959; Mabaye 1971; Fryer and Iles 1972; Lowe-McConnell 1975, 1982; Balarin and Hatton 1979; Palada-de Vera and Eknath 1993; Toguyény *et al.* 1996, 1997).

The causes of male growth superiority in cichlids have been examined; however, no single explanation of sexual dimorphism in size has been widely accepted. One hypothesis is that tilapia females put so much more energy into egg production, producing eggs at very frequent intervals, which may result in costs to growth; also the females almost cease to feed while mouthbrooding their eggs and young (Lowe-McConnell 1975). Another is that male sex hormones have an anabolic or growth promoting effect, which could result in the higher growth of males (Donaldson *et al.* 1979; Ufodike and Madu 1986). In addition, thyroid hormones (*T*$_3$ and *T*$_4$) also participate in regulating growth and development. Toguyény *et al.* (1996, 1997) observed, in Nile tilapia, that plasma *T*$_3$ levels were higher in males than females, which could account for the males’ growth advantage. It was also suggested that the difference in growth may be related to a sex-linked genetic characteristic which gives the male an advantage either through efficiency of food conversion, or through aggressive feeding behavior (Mabaye 1971). Behavioral activity and its association with larger-sized males compared to females is an area that remains to be explored. Toguyény *et al.* (1997) observed, in mixed sex groups of Nile tilapia, an increase in activity and a decrease in growth; however, no connection was made between the higher growth of males and their activity level. Therefore, more experimentation is needed to study the relationship between growth and activity level in both sexes.

**Nile tilapia (*Oreochromis niloticus*)**

Nile tilapia has dominated global tilapia culture since the 1980s, and its share of total tilapia production has increased dramatically from 33% or 66,000 t in 1984 to 72% or 474,000 t in 1995 (Rana 1997). However, Pullin and Capili (1988) found that little attention had been given to the genetic improvement of farmed Nile tilapia and that more investment in research for the in genetic improvement was needed. Based upon these findings, the International Center for Living Aquatic Resources Management (ICLARM) and its collaborators initiated the Genetic Improvement of Farmed Tilapias (GIFT) project in the Philippines. Four new wild founder populations of Nile tilapia (from Egypt, Ghana, Kenya, and Senegal) and populations of four strains of Nile tilapia in current use by farmers in Asia (‘Israel’, Singapore, Taiwan, and Thailand) were assembled. The genetic material from the best families of all strains were incorporated, according to their performance.

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3 Note that this should result in female fish of other species also being smaller than the males. However, females are larger than males in about 70% of all species of fishes (Pauly, 1994)
rankings, into a synthetic strain termed ‘GIFT’ strain. This synthetic strain has since been subjected to
selective breeding for good growth (Pullin 1998), which resulted in the GIFT strain having a higher growth
potential that of some of the strains farmed in Asia (ICLARM-ADB 1998; Pullin 1998).

Objective of the study

In culture ponds of the Philippines, fish of the GIFT strain of Nile tilapia were observed to grow faster than
control fish (Pullin 1998). To examine these growth differences in Nile tilapia, the following questions were
addressed through a first set of experimental studies: Do the differences in the growth rate of GIFT and
control fish persist under controlled laboratory conditions? Does the difference apply to both male and
female? Can any growth differences be related to a difference in behavioral activity, and the onset of sexual
maturity? To examine the relationship between growth rate and the onset of sexual maturity in both strains of
Nile tilapia, nesting activity, a behavior that is often the first indication of the sexual maturity of fish, was
studied.

The second set of experiments examined, in more details, the differences in the offensive aggression between
male fish of both strains. In a first experiment, male control fish were observed to perform more agonistic
behaviors than male GIFT fish. However, the effect that social interactions in mixed sexed groups have on
behavioral measures (see Toguyëni et al. 1997) may have complicated the results of the first experimental
study. Therefore, offensive aggression was quantified using the mirror image stimulation (MIS) tests (Gallup
1968). In juvenile coho and chinook salmon, the reactions to mirror images have been correlated with the
reactions to conspecifics (Rosenau 1984; Taylor and Larkin 1986; Rosenau and McPhail 1987; Taylor 1988;
Swain and Holtby 1989). Fish that spend more time performing mirror-elicited agonistic behaviors were also
found to be more aggressive in social interactions under more natural circumstances. These tests have the
advantage that individuals are tested against ‘opponents’ of exactly the same size and motivational state and
that adequate replication is practical (Swain and Riddell 1990). Male fish were only examined in this MIS test
because female fish were observed to perform relatively little agonistic behavior in mixed sexed groups
(Experiment 1), and in all-female stock aquaria (Boyzynski pers. obs.).

MATERIALS AND METHODS

Experimental animals

The two strains of Nile tilapia (Oreochromis niloticus), a fish of African origin, were imported into Vancouver,
Canada in early 1997 from the National Freshwater Fisheries Technology Research Center (NFFTRC), Muñoz,
Nueva Ecija, then jointly operated by ICLARM and the Bureau of Fisheries and Aquatic Resources (BFAR) of
the Philippines. The two strains were 4th generation of GIFT fish (see Introduction for background on Nile
tilapia) and ‘control’ Nile tilapia from Bulacan Province, Philippines, typical of those fish farmed in Asian
countries where selective breeding had not been widely applied.

Holding and experimental facilities

On arrival at the University of British Columbia, the fish were placed in 55 and 102 liter (L) stock tanks with
similar fish densities (approximately 5.5 L of water per fish) for a five week period to acclimatize the fish to the
laboratory conditions; the fish were then transferred to the experimental aquaria. All experimental aquaria
were maintained at 24.0 ± 0.5°C; the water temperature was similar to both pond sources in the Philippines
(i.e., 24-25°C). The temperature of the water in the experimental tanks was maintained by the use of a room
heater which kept the room temperature at approximately 27°C. Each experimental tank, with dimensions of
61.0 cm x 30.5 cm x 30.5 cm, was provided with a layer of gravel (depth of 2.5 cm), and a box charcoal filter.
All four sides of the tanks were covered with beige paper to prevent visual interference between neighboring
fish. Illumination was provided, over a 12-h photoperiod, by fluorescent lights mounted 2 m above each row of
tanks. The light strips were positioned upwards to minimize light reflection from the water surface from
entering lens of the video camera during recording. A color pro843 RCA video camera was supported by a 4-
wheeled aluminum stand that enabled it to be positioned lens down approximately 75 cm above the rim of
each experimental tank. During behavioral recording, two extra light strips, housed in a wooden frame, were
placed on either side of the row of aquaria to allow the fish to be seen clearly. These two extra light strips were
turned on 30 min prior to the observation sessions to acclimatize the fish to the higher light intensity. The
Fish were fed commercially prepared catfish feed (Otter Co-op, Aldergrove, British Columbia) at 3% wet weight of fish daily. The quantity of feed given was adjusted monthly following the recording of standard length and weight of each fish.

**Fish identification**

The fish were marked by attaching a colored bead to each individual. The beads were attached 10 days prior to the start of the behavioral recordings. The fish were anaesthetized by being immersed in a buffered 0.03% w/v solution of methane tricaine sulfonate (MS 222, Syndel Laboratories, Vancouver). When a fish was nearly motionless, on its side, and respiring slowly, the fish was removed from the solution and placed on a moist sponge. A 0.25 mm diameter nylon monofilament, with one bead tied onto one end, was sewn through the musculature at the front end of the dorsal fin using a sewing needle. The bead was secured onto the fish as described in Kroon (1997). The fish was returned to the freshwater and allowed to recover. Five light-colored beads were used: yellow, white, blue, green, and pink. These bead colors were chosen because they were in sharp contrast to the dark surroundings (i.e., dark body coloration and sand).

The presence of brightly colored beads on the fish apparently did not change the motivational state of the neighboring fish; there appeared to be no increase in the frequency of agonistic acts directed towards beaded fish (Boyzynski pers. obs.). It was important to resolve this issue because body color patterns are important in the visual communication of cichlids and the pattern of coloration changes according to the motivational state of the fish (Billy 1982; Nelissen 1991). For a more detailed description of color patterns in tilapias see Billy (1982).

**Determination of sex**

The sex of the fish was initially determined by the external examination of the genital papilla (Afonso and Leboute 1993) and then verified later by the dissection of the gonads. The distinctive features of the genital papilla of the male and female tilapia are described by Maar et al. (1966). Briefly, the male has two orifices situated just forward of the anal fin. One is the vent, the other is the urogenital aperture which usually forms into a small papilla. The female, in contrast, has three orifices, namely the vent, a transverse genital opening and a microscopic urinary orifice, which is scarcely visible to the naked eye (Balarin and Hatton 1979). The anaesthetized fish was placed belly-up on a moist sponge and a dye (potassium permanganate) was applied onto the genital papilla with a Q-tip, as suggested by L.O.B. Afonso (pers. comm. to the first author). This dye was used to highlight a slit (genital opening) present only in the females (Afonso and Leboute 1993). The anaesthetized fish was then placed under a dissecting microscope (magnification: 7-10X) to inspect the genital papilla. A fish was considered to be a female when the slit was observed. The sex determination procedure commenced on May 19, 1997 and was repeated and thereby verified during the monthly recordings of the weight and length measurements.

**Behavioral measures**

Detailed descriptions of cichlid behavior can be found in Baerends and Baerends-van Roon (1950), Billy (1982), and Fryer and Iles (1972). For the purpose of this experiment, the activity was measured on the basis of the following twelve behaviors.

1) **Swimming**: a movement of the fish in any direction in the water column without any interactions with other fish;
2) **Resting**: a fish stays in the same position, either in the water column or on the gravel bottom, long enough for the computer key used to encode resting behavior to be pressed by the observer;
3) **Chasing/Escaping**: a fish swimming after another fish at a high velocity is described as chasing, while escape behavior is carried out by the fish swimming away from the aggressor;
4) **Tail-beating**: a fish presents the lateral aspect of its body to an opponent, head to tail, and uses its caudal fin to beat the water sideways over the head of its opponent (Baerends and Baerends-van Roon 1950; Billy 1982; Fryer and Iles 1972). The tail-beating individual does not actually touch the opponent. Tail-beating is used as a threat signal by a territorial male towards an intruding male (Billy 1982); presumably, this act communicates the animal’s strength (Baerends and Baerends-van Roon 1950). Tail-beating also serves as a courtship signal by a territorial male towards a female entering his territory (Billy 1982);
5) **Nipping**: a bite directed towards a fin and/or the body of a neighbouring fish. Occasionally, nipping results in fin amputation and body scarring (Billy 1982);

6) **Confronting**: occurs between territorial males during boundary disputes. Opposing males rush at each other ending their charges at the common boundary (nest rim). The males then oscillate back and forth in synchrony, with one male (fins collapsed) retreating while its opponent (fins raised) advances a few centimetres. This back and forth motion is completed several times in rapid succession, after which the males separate or attack (e.g., jaw lock) (Billy 1982);

7) **Jaw lock**: the fish grip each other’s mouth, and start pushing and pulling each other to and fro (Fryer and Iles 1972);

8) **Opercular flare**: a fish erects the operculae and branchiostegal membrane, and reveals its dorsally-situated black opercular spots;

9) **Gulping**: a fish swims to the water surface and takes in surface water with its mouth. This behavior increases oxygen uptake, i.e., complements gill breathing (Weber and Kramer 1983);

10) **Feeding**: a fish picks up sand with its mouth, sifts (i.e., separates food particles from sand), and then drops sand indiscriminately;

11) **Nesting**: a fish swims head down into the substrate, secures a mouthful of sand, swims a short distance from the centre of the pit, and spits out the substrate. In contrast to feeding, no sifting is performed. The displaced substrate is deposited on the edge of a territory, where it accumulates and forms a raised rim around the nest. This raised rim defines territorial boundaries. Localized digging produces a pit which a male occupies and defends from intruders while attempting to attract spawning partners. Nesting is used to maintain the nest rim and to remove debris from the pit. Each male digs throughout its residency in a territory, with the frequency of digging at a peak when the territory is being established. The female fish also nest, but only in the later stages of courtship prior to spawning (Billy 1982).

The total duration of swimming and resting was recorded, while the number of bouts of chasing, escaping, tail-beating, nipping, confronting, jaw-locking, opercular flaring, gulping, feeding, and nesting were recorded. The data on locomotor and agonistic behaviors were then analysed using The Observer version 3.0 computer software (Noldus Information Technology, Wageningen, Netherlands).

**Experimental procedures**

Small mixed sex groups (5 fish per tank) of GIFT and control strains were established in 55 L aquaria on March 7, 1997. At this time, the mean weight and standard length of the mixed sex GIFT and control fish were $5.3 \pm 1.6$ g and $5.3 \pm 0.6$ cm, and $4.8 \pm 1.8$ g and $5.1 \pm 0.7$ cm, respectively. Initially, the fish could not be sexed, and hence the mixed sex design. However, as the experiment progressed and the fish grew, sex determination became possible.

At the start of the experiment (April 19th), each aquarium contained five fish. However, as the experiment progressed, some aquaria had less than five fish present as a result of mortality. The aquaria with four or five fish were retained in the experiment. Groups with fewer than four fish were excluded. Preliminary observations showed that the fish in aquaria with four or five fish had similar activity levels, while the surviving fish in the tanks with less than four fish were very aggressive. This resulted, in most cases, in only one fish remaining in the tank.

On day 1, the weight and standard length measurements were recorded. The locomotor and aggressive activities of the control and GIFT fish were video recorded on day 10 and day 12 (trials #1 and 2, respectively) during a 300 second observation period. On day 31, length and weight measurements were repeated. This experimental schedule was repeated three times over the three-month study period (April-June). The mean growth and behavioral measurements of all fish in an experimental group were compared, instead of individual measures because growth and behavior of individual fish in each aquarium were not independent of the behavior of other members of the group. Due to the fact that individual fish in the video recordings of the first trial in April could not be identified, only trial #2 could be used to compare activity levels between the female and male fish of each strain. Furthermore, size-specific mortality in male and female fish could only be examined in May and June because, in April, the sex of the fish could be determined neither by the external examination of the genital papilla due to the small size of fish, nor by the dissection of the gonads, due to the cannibalistic practice of live tank mates towards dead fish.
Aggressive behavior of males from the control and GIFT strains in response to a mirror image was also examined. Biting and tail-beating behaviors were distinguished in the MIS tests. These two behaviors are similar to the nipping and tail-beating behaviors previously mentioned, except that they are directed towards a mirror instead of a conspecific.

Small groups (5 fish per tank) of mixed sex GIFT and control strains were re-established in 55 L aquaria on November 15, 1997. These fish had been previously used in the growth experiment approximately four and a half months earlier. On day 1 (Nov. 19th), the weight and standard length measurements of all male fish were recorded; during the two week study period, the mean weight and standard length of the male control and GIFT fish were 26.2 ± 9.8 g and 9.5 ± 1.3 cm, and 34.0 ± 10.6 g and 10.2 ± 1.2 cm, respectively. On day 3, one day prior to the start of behavioral observations, male control and GIFT fish were individually placed in 55 L aquaria; the mean water temperature of the experimental aquaria was 23.7 ± 0.3°C during the two week study period. Each experimental aquarium was divided in two by an opaque partition; the fish was placed on the left side with a boxed filter, while the mirror was positioned on the right side behind the partition.

On day 4, at the start of each behavioral session, the partition was lifted exposing the mirror to the fish. A 300 second observation period began when the male fish was observed, on the video monitor, swimming towards the mirror and performing either biting or tail-beating behaviors. At the end of the day when all behavioral sessions were recorded, the fish were returned to their appropriate stock tanks and new fish were transferred to the experimental aquaria for the next day. Each male was tested twice about a week apart between the two trials, so the data provided is a mean of the two trials.

**Statistical analyses**

Linear regressions were used to test for significant differences in the growth curves (weight and length). The Mann-Whitney U-test was used in the comparison of independent measures of fish from the GIFT and control strain. These tests were one-tailed unless otherwise stated. The chi-square goodness of fit test was used to determine if there were significant differences between the actual number of fish from four experimental groups (i.e., female control, male control, female GIFT and male GIFT) that performed behavioral activities, and a theoretically even distribution. If the chi-square analysis detected significant departures from the even distribution, it was subdivided to determine whether the significant difference between observed and expected frequencies was concentrated in certain of the experimental groups, or whether the difference was due to the effects of the data in all of the four experimental groups (Zar 1996). When the observed frequencies were small, the use of the two-tailed Fisher exact test was preferred over the chi-square analysis. The level of significance was set at $p = 0.05$ for all statistical analyses.

**RESULTS**

**Growth, activities and sexual maturation in the control and GIFT strains of Nile tilapia**

During the three-month study period (April-June), the GIFT fish were observed to have significantly faster growth rates than the control fish (one-tailed comparison of simple linear regression equations; weight: $p<0.05$, length: $p<0.005$) (Figure 1). GIFT fish gained 4.9 g-month$^{-1}$ and increased in length by 0.9 cm month$^{-1}$, while the values for the control fish were 3.2 g-month$^{-1}$ and 0.7 cm-month$^{-1}$, respectively. Furthermore, the weight and length of the GIFT fish were found to be significantly greater than the control fish at each measurement (Figure 1).

**Table 1.** Total time (mean ± SD) two strains of juvenile Nile tilapia (control and GIFT) performed swimming and resting acts each month of the three-month study. Each month two 300 second behavioural trials were recorded one day apart. All experimental aquaria had four or five fish present and the number of aquaria used is represented by the n-values (data from the aquaria with less than four fish present were not used). The Mann-Whitney U-test (one-tailed) was used to test for significant differences in the total time the control and GIFT fish allotted to swimming and resting acts each month. * $p<0.025$, ** $p<0.01$, *** $p<0.005$, **** $p=0.0025$.

<table>
<thead>
<tr>
<th>MONTH</th>
<th>STRAINS OF NILE TILAPIA</th>
<th>TOTAL TIME (SEC) SPENT PERFORMING BEHAVIOURS PER 300 SECOND TRIAL (MEAN ± SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Swimming</td>
</tr>
<tr>
<td>April</td>
<td>control (n=13)</td>
<td>76.4 ± 81.0***</td>
</tr>
<tr>
<td></td>
<td>GIFT (n=10)</td>
<td>19.3 ± 33.0</td>
</tr>
<tr>
<td>May</td>
<td>control (n=10)</td>
<td>51.9 ± 45.8*</td>
</tr>
<tr>
<td></td>
<td>GIFT (n=9)</td>
<td>10.7 ± 12.6</td>
</tr>
<tr>
<td>June</td>
<td>control (n=7)</td>
<td>41.4 ± 46.1</td>
</tr>
<tr>
<td></td>
<td>GIFT (n=9)</td>
<td>19.1 ± 27.1</td>
</tr>
</tbody>
</table>
The GIFT fish also spent less time swimming and more time resting than the control fish (Table 1). The differences in swimming/resting behaviors between the control and GIFT fish were significant in April and May, but not in June (Table 1). The time the control fish spent swimming decreased by 46% during the three-month period, while the level of swimming activity for the GIFT fish remained relatively constant (Table 1). In contrast, the control fish increased the time spent resting by 18% during the study, while the resting values for the GIFT fish again remained relatively constant (Table 1).

Moreover, control fish performed more chasing and escaping behaviors than the GIFT fish (Table 2). The differences were significant in April and May, but not in June (Table 2). The frequency of chasing and escaping exhibited by control fish increased in May by 23% and 10% of April values, respectively, and then declined in June by 55% and 52%, respectively (Table 2). In the GIFT fish, the frequency of chasing increased by 29% during the study, while escaping increased in May by 20% of April values, and then declined in June.

Figure 1. Upper left: Weight (mean ± SD) and Lower left: Length (mean ± SD) of fish from two strains of Nile tilapia (control and GIFT). All experimental aquaria had four or five fish present and the number of aquaria used during the study period is represented by the n-values (data from aquaria with less than four fish present were not used in the mean weight calculations). The Mann-Whitney U-test (one-tailed) was used to test for significant differences in the weight and length, respectively, of fish of both strains. (*p<0.05, **p<0.025, ***p<0.01, ****p=0.005, *****p<0.0025). Upper right: Weight (mean ± SD) and Lower right: Length of females and males from two strains of Nile tilapia (control and GIFT). The numbers of males and females from both strains used during the three-month study is represented by the n-values. The Mann-Whitney U-test (one-tailed) was used to test for significant differences between the weight of females and males of the same strain (GIFT: *p<0.05, **p<0.025, ***p<0.01, ****p=0.005, *****p<0.0025), females or males of different strains (males: +p<0.01, ++ P <0.001, +++ p<0.0005, ++++p<0.0025), and females and males of different strains (GIFT male vs control female: ‡p<0.025, ‡‡p<0.01, ‡‡‡p<0.0025, ‡‡‡‡p<0.005)
by 37% (Table 2). A higher frequency of tail-beating was characteristic of the control fish compared to the GIFT fish; the differences were only significant in April (Table 2). Tail-beating frequency of control fish increased by 61% during the study while, in GIFT fish, the frequency increased in May by 327% of April values, and then declined by 70% in June (Table 2). Furthermore, nipping frequency was found to be significantly higher in the control fish than the GIFT fish during the three-month study period. The nipping frequency of control and GIFT fish increased in May by 169% and 129% of April values, respectively, and then declined in June by 73% and 94%, respectively (Table 2). Only the control fish performed confronting and jaw-locking behaviors and the frequency of confronting declined by 73% during the study, while jaw-locking remained relatively constant (Table 2). No opercular flares were performed during the behavioral trials so this behavior was excluded from analyses.

Gulping was also found to be mostly performed by the control fish (Table 2). An increase (114%) in the frequency of gulping was observed in May, and then dropped to zero in the behavioral sessions of June (Table 2). Feeding behavior was performed more often by control fish than GIFT fish especially in May, but the differences were not significant (Table 2). The feeding frequency of control fish increased in May by 150% of April values while, in the GIFT fish, the frequency remained relatively constant (Table 2). In the behavioral sessions of June, no feeding behavior was recorded by either control or GIFT fish (Table 2).

As the experiment progressed and the sex of each fish could be determined, the weight and length, and activity levels of male and female fish of both strains were compared. During the three-month study period, the male GIFT fish were observed to have a faster growth than the female GIFT fish (Figure 1). The difference was significant only for growth in length (one-tailed comparison of simple linear regression equations; p<0.05). The male GIFT fish gained 5.8 g·month⁻¹ and increased in length by 1.0 cm/month, while the corresponding values for the female GIFT were 3.9 g·month⁻¹ and 0.9 cm·month⁻¹, respectively. In contrast, the growth rates of the male and female control fish were similar (Figure 1). The male control fish gained 3.1 g·month⁻¹ and increased in length by 0.7 cm·month⁻¹, and the values for the female control fish were 3.2 g·month⁻¹ and 0.7 cm·month⁻¹, respectively. The growth rate in weight of female GIFT was slightly higher than the male and female control fish (Figure 1). However, in the male GIFT, the growth rate in weight was found to be significantly higher (one-tailed comparison of simple linear regression equations; comparison of female and male control to male GIFT fish: p<0.05, p<0.05, respectively). Furthermore, the growth rates in length of the female and male GIFT were significantly different than that of the male and female control fish (one-tailed comparison of simple linear regression equations; comparison of female and male control to female GIFT fish: p<0.025, p<0.005, respectively; comparison of female and male control to male GIFT fish: p<0.025, p<0.025, respectively).

The weight and length of the male GIFT were significantly higher than the female GIFT during the three-month study period. In contrast, the weight of the male control was slightly lower than the female control during the study. The length of the male control also was slightly lower than the female control fish in April, but then increased slightly above length values of female control in May and June (Figure 1). Furthermore, the weight and length of male GIFT fish were significantly greater than either the male or female controls, while the measurements of the female GIFT fish were slightly higher than either the female or male controls (Figure 1). The only exception was in April where the weight of the female GIFT fish was found to be slightly lower than in the female controls.

The male control fish also spent more time swimming and less time resting than the female control fish. However, a significant difference in the allotment of time to swimming and resting was only found in May (Table 3). In contrast, the male GIFT fish spent less time swimming and more time resting than the female GIFT fish, except in April (Table 3). The differences in swimming and resting behaviors were significant only in June (Table 3). Furthermore, the male control fish spent significantly more time swimming and less time resting than either female or male GIFT fish (Table 3). The female control fish also spent more time swimming and less time resting than either female (except in June) or male GIFT fish (Table 3). The differences in swimming and resting behaviors between the female control and male GIFT fish were significant throughout the three-month study. The differences in swimming behavior between the female control and GIFT fish were only significant in April, while the differences in resting behaviors were significant in both April and May (Table 3).
Table 2. Number of bouts of locomotory and agonistic behaviours (mean ± SD) the control and GIFT strains of juvenile Nile tilapia performed each month of the three-month study. Each month two 300 second behavioral trials were recorded one day apart. The number of control and GIFT aquaria used each month is represented by the n-values. The Mann-Whitney U-test (one-tailed test, except for gulping and feeding behaviours) was employed to test for significant differences between the number of acts performed by the fish from the control and GIFT aquaria for each month. * p=0.05, ** p<0.025, *** p<0.01, **** p<0.005, ***** p<0.0025.

<table>
<thead>
<tr>
<th>MONTH</th>
<th>STRAINS OF NILE TILAPIA</th>
<th>NUMBER OF BOUTS OF LOCOMOTORY AND AGONISTIC BEHAVIORS (MEAN ± SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td>April</td>
<td>control (n=13)</td>
<td>1.2 ± 1.3*** 1.7 ± 1.8***** 0.6 ± 0.8** 0.3 ± 0.3* 0.1 ± 0.3 0.01 ± 0.03 1.0 ± 3.1 0.2 ± 0.4 0.1 ± 0.3</td>
</tr>
<tr>
<td></td>
<td>GIFT (n=10)</td>
<td>0.2 ± 0.4 0.3 ± 0.5 0.1 ± 0.4 0.1 ± 0.1 0 0 0 0 0</td>
</tr>
<tr>
<td>May</td>
<td>control (n=10)</td>
<td>1.5 ± 1.4*** 1.0 ± 1.7***** 0.9 ± 1.2 0.7 ± 0.6**** 0.1 ± 0.2 0.02 ± 0.06 2.1 ± 5.3 0.4 ± 1.0 0.2 ± 0.5</td>
</tr>
<tr>
<td></td>
<td>GIFT (n=9)</td>
<td>0.2 ± 0.5 0.3 ± 0.8 0.5 ± 1.4 0.2 ± 0.2 0 0 0.01 ± 0.03 0.1 ± 0.3 0.01 ± 0.03</td>
</tr>
<tr>
<td>June</td>
<td>control (n=7)</td>
<td>0.7 ± 0.9 0.9 ± 1.4 1.0 ± 2.1 0.2 ± 0.3** 0.03 ± 0.05 0 0 0 0.4 ± 0.8</td>
</tr>
<tr>
<td></td>
<td>GIFT (n=9)</td>
<td>0.2 ± 0.6 0.2 ± 0.5 0.1 ± 0.3 0.01 ± 0.03 0 0 0 0 0.03 ± 0.10</td>
</tr>
</tbody>
</table>
Table 3. Total time in seconds (mean ± SD) performing swimming and resting acts and number of bouts of agonistic and escape behaviours (mean± SD) performed by the female and male juvenile Nile tilapia (control and GIFT strains) each month of the three-month study. Each month two 300 second behavioral trials were recorded one day apart. The five behaviors included under the agonistic category are chasing, tail-beating, nipping, confronting, and jaw-locking. Due to unforeseen circumstances, only data from the behavioral trial #2 in April were tabulated. The number of female and male fish of both strains used each month is represented by n-values (i.e., # of fish in April, May, June, respectively).

<table>
<thead>
<tr>
<th>SEXES/STRAINS OF NILE TILAPIA</th>
<th>Female control (n=18, 14, 10)</th>
<th>Male control (n=39, 31, 22)</th>
<th>Male GIFT (n=23, 22, 22)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>April</td>
<td>May</td>
<td>June</td>
</tr>
<tr>
<td>Swimming</td>
<td>70.3 ± 79.8</td>
<td>35.1 ± 43.2</td>
<td>19.2 ± 16.5</td>
</tr>
<tr>
<td>Female GIFT (n=22, 23, 23)</td>
<td>35.1 ± 55.1</td>
<td>11.5 ± 12.7</td>
<td>25.1 ± 27.6</td>
</tr>
<tr>
<td>Resting</td>
<td>221.0 ± 81.1</td>
<td>256.5 ± 52.3</td>
<td>279.7 ± 18.2</td>
</tr>
<tr>
<td>Agonistic</td>
<td>0.1 ± 0.1</td>
<td>0.1 ± 0.3</td>
<td>0.2 ± 0.6</td>
</tr>
<tr>
<td>Escaping</td>
<td>3.0 ± 3.7</td>
<td>1.6 ± 1.9</td>
<td>0.6 ± 1.0</td>
</tr>
<tr>
<td>Male GIFT (n=23, 22, 22)</td>
<td>202.4 ± 97.6</td>
<td>218.0 ± 69.7</td>
<td>234.8 ± 71.4</td>
</tr>
<tr>
<td>Swimming</td>
<td>70.3 ± 79.8</td>
<td>35.1 ± 43.2</td>
<td>19.2 ± 16.5</td>
</tr>
<tr>
<td>Resting</td>
<td>221.0 ± 81.1</td>
<td>256.5 ± 52.3</td>
<td>279.7 ± 18.2</td>
</tr>
<tr>
<td>Agonistic</td>
<td>0.1 ± 0.1</td>
<td>0.1 ± 0.3</td>
<td>0.2 ± 0.6</td>
</tr>
<tr>
<td>Escaping</td>
<td>3.0 ± 3.7</td>
<td>1.6 ± 1.9</td>
<td>0.6 ± 1.0</td>
</tr>
</tbody>
</table>
During the three month study, the total time male and female control fish spent swimming declined by 35% and 73% of starting (April) values, respectively, while the time spent resting increased by 16% and 27%, respectively (Table 3). In contrast, the amount of time the male and female GIFT fish spent swimming declined in May by 72% and 67% of the April values, respectively, but then increased in June by 29% and 119%, respectively (Table 3). Moreover, the total time male and female GIFT fish spent resting increased from April to May by 10% and 9%, respectively, but then declined slightly (i.e., by 1% and 4%, respectively) in June (Table 3).

Male fish performed more agonistic behaviors than the female fish (except in June between male GIFT and female control). However, only the differences between the male control and female GIFT fish were significant (Table 3). When males of both fish strains were compared, the male control performed more agonistic behavior than the male GIFT fish (Table 3). The differences were significant in May and June, but not in April. When the females were compared, the control also performed more agonistic behavior than the GIFT fish, but the differences were not significant (Table 3). The frequency of agonistic behavior exhibited by male control, and female and male GIFT fish increased in May by 65%, 100% and 4% of the April values, respectively, then declined in June by 27%, 33% and 48%, respectively, while the frequency of agonistic behavior exhibited by female control increased by 243% during the study. The number of male control fish performing agonistic behaviors was significantly greater than the number of female control, and male and female GIFT fish combined (corrected chi-square analyses: April, \( p<0.01 \); May, \( p<0.001 \); June, \( p<0.005 \)).

Escape behavior was performed by both female and male fish (Table 3). Both the male and female control fish performed more escape behavior than the male and female GIFT fish (Table 3). The differences in escape behavior between the female control and GIFT fish were only significant in April, while the differences between female control and male GIFT were significant in both April and May (Table 3). In the comparison of the male control to the female and male GIFT, significant differences were found in April and June, and May and June, respectively (Table 3). When female and male control fish were compared, male fish exhibited less escape behavior in April than female fish, but in May and June, male fish performed more escape behavior than female fish. In contrast, male GIFT fish exhibited more escape behavior in April, but performed less escape behavior than female GIFT fish in May and June. No significant difference in escape behavior was found between male and either the control or GIFT strain. The frequency of escape behavior exhibited by the female and male control, and the female and male GIFT fish declined during the study by 82%, 47%, 42%, and 80% of the April values, respectively. The number of male control fish performing escape behavior was significantly greater than the number of female control, and male and female GIFT fish combined (corrected chi-square analyses: April, \( p<0.025 \); May, \( p<0.001 \); June, \( p<0.025 \)).

Table 4. Number of bouts of locomotory behaviors (mean ± SD) performed by the female and male juvenile Nile tilapia (control and GIFT strains) each month of the three-month study. Each month two 300 second behavioral trials were recorded one day apart. Due to unforeseen circumstances, only data from the behavioral trial #2 in April were tabulated. The number of female and male fish of both strains used each month is represented by the n-values. The Mann-Whitney U-test (two-tailed test, except for nesting behaviour) was employed to test for significant differences between the number of acts performed by the female and male fish from the control and GIFT aquaria for each month.

<table>
<thead>
<tr>
<th>Month</th>
<th>Sexes/strains Nile tilapia</th>
<th>Number of bouts of locomotory behaviors (mean ± SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Gulping</td>
</tr>
<tr>
<td>April</td>
<td>female control (n=18)</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>male control (n=39)</td>
<td>2.7 ± 13.4</td>
</tr>
<tr>
<td></td>
<td>female GIFT (n=22)</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>male GIFT (n=23)</td>
<td>0</td>
</tr>
<tr>
<td>May</td>
<td>female control (n=14)</td>
<td>1.3 ± 4.7</td>
</tr>
<tr>
<td></td>
<td>male control (n=31)</td>
<td>2.8 ± 9.7</td>
</tr>
<tr>
<td></td>
<td>female GIFT (n=23)</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>male GIFT (n=22)</td>
<td>0.02 ± 0.11</td>
</tr>
<tr>
<td>June</td>
<td>female control (n=10)</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>male control (n=22)</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>female GIFT (n=23)</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>male GIFT (n=22)</td>
<td>0</td>
</tr>
</tbody>
</table>
Gulping was mostly performed by the male control fish; however, in May, the female control fish also performed gulping behavior (Table 4). A slight increase in the gulping frequency of male control and GIFT fish was observed in May, but it dropped to zero in June. The number of male control fish gulping was greater than either the number of female control, male GIFT or female GIFT fish; however, the differences were not significant.

A greater number of feeding bouts were performed by the male control and GIFT fish than the female fish; however, in May, the feeding frequency of the female control was higher than male GIFT. The feeding frequency of male control fish also was greater than male GIFT fish; the difference was significant only in May (Table 4). In contrast, female GIFT performed more feeding bouts than female control in April, while female control performed more feeding bouts than female GIFT in May. The feeding frequency of male controls and of female and male GIFT fish declined in May by 4%, 50%, and 63% of April values, and then dropped to zero in June. The number of male control fish feeding during the behavioral trials was significantly greater than the number of female control, and male and female GIFT fish combined (corrected chi-square analyses: May, p<0.01).

To assess the sexual maturity of fish, nesting behaviors, and the number of nests present in both the control and GIFT aquaria were recorded during the three-month study period. Nests were first observed on April 1st in three of the control tanks; and by the eve of the first behavioral trial in April, nests were present in 11 of the 13 control tanks compared to only 1 GIFT tank out of a total of 10. During the three-month study period, nesting behavior was performed more frequently by the control fish than the GIFT fish, but the differences were not significant (Table 2). A large increase (236%) in nesting frequency of control fish was observed during the study, while the nesting frequency of GIFT fish increased slightly (Table 2). Only males of both the GIFT and control strains were observed to perform nesting behavior. The nesting frequency of male control increased from May to June by 45%, while the frequency of male GIFT increased slightly (Table 4). The number of male control fish nesting was greater than either the number of female control, male GIFT or female GIFT fish; however, the differences were not significant. Furthermore, significantly more nests were present in the control aquaria than GIFT aquaria during the three-month study (Figure 2). Control fish also built more nests earlier in study (i.e., April) than GIFT fish; it took the GIFT fish until June to reach the number of nests found in the control aquaria in April (Figure 2).
Size-specific mortality was observed in both strains (Table 5). The dead control fish had lower weights and lengths than the live fish present in the same experimental aquaria; the differences were significant in May and June, but not in April (Table 5). The dead GIFT fish also had smaller weight and length measurements than the live fish in the same experimental aquaria; however, no rigorous analyses could be performed due to the low number of dead fish (Table 5). The weight and length of dead and live male control fish were significantly different in both May and June, while the dead and live female fish were similar (Table 6). Therefore, size-specific mortality occurred only in male fish.

**Aggressive behavior of males from the control and GIFT strains of Nile tilapia in response to a mirror image**

During the two-week study period, the male control fish performed a higher number of bouts of mirror-directed biting and tail-beating than the male GIFT fish (Figure 2). Only the differences in mirror-directed biting were significant (Figure 2).

**DISCUSSION**

Under laboratory conditions, the GIFT fish grew faster than the fish from the control strain. It was not surprising that growth performance was higher in the GIFT than control fish, as the former had been subjected to intentional selection for that trait (Pullin, 1998 and see Introduction for background on Nile tilapia). The results from the behavioral experiment on Nile tilapia suggest that behavioral activity contributes to this effect on growth.

The fast growth of GIFT fish was associated with a lower activity level compared to control fish. GIFT fish performed less swimming and more resting behavior than control fish. These findings are similar to the study by Koebele (1985) on juvenile *Tilapia zillii*, which suggested that an increase in activity such as swimming may have resulted in a slight decrease in their mean growth. The fast-growing GIFT fish also exhibited a lower frequency of agonistic behavior than the slow-growing control fish. This connection between growth and aggression has been previously documented. Ruzzante and Doyle (1991) observed in the medaka, *Oryzias latipes*, that fish ‘indifferent’ to other neighboring fish (i.e., not involved in aggressive behavior) grew the fastest. In addition, a negative correlation between aggression and growth was found in the tilapia hybrid, *Oreochromis mossambicus* x *O. hornorum* (Robinson and Doyle 1990) and Atlantic salmon (Holm and Fernö 1986). Swimming activity, and especially agonistic interactions are energetically costly, and thus passive (i.e., GIFT) fish, with a relatively lower metabolic expenditure, should gain a growth advantage over active (i.e., control) fish. Increased demand for energy during exercise has been confirmed in several studies on oxygen consumption, which reflect behavioral activities in fish (Beamish 1980; Nahhas *et al.* 1982; Butler 1985).

The fact that the more active control fish have reduced compared with GIFT fish is well explained by the oxygen-limitation hypothesis proposed by Pauly (1981; see also Pauly 1984, 1994; 2010). It has been observed by Stewart *et al.* (1967), that largemouth bass held in hypoxic waters usually had a lower percent dry weight than fish held at concentrations near the air-saturation level. Balarin and Hatton (1979) found, in tilapia, that at low oxygen levels, growth decreased; Kolding *et al.* (2008) obtained similar results. Thus, anything, in a given population, that causes a higher metabolic expenditure (e.g., high activity level), will result in a reduced fish size.

Gulping was mostly performed by the active, slow-growing control fish. It has been observed that aquatic surface respiration (i.e., gulping) is initiated at higher oxygen concentrations than necessary for survival, and thus this behavior can provide an energetic advantage to fish (Weber and Kramer 1983). The fish approaching the water surface and aerating their gills with oxygen-saturated water increase oxygen uptake rate and/or decrease the work required for ventilation, as compared to subsurface respiration (Weber and Kramer 1983). An increase in the oxygen uptake rate of fish would permit greater food intake (Weber and Kramer 1983; Pauly 2010). The control fish was also observed to perform more feeding behavior than the GIFT fish. Intraspecific comparisons between wild and hatchery-reared Atlantic salmon have shown that wild fish generally feed more than hatchery fish (Fenderson *et al.* 1968; Sosiak *et al.* 1979).
A likely explanation for the higher gulping of control fish in April and May is that their higher oxygen requirements were due to their high activity and feeding frequency compared to GIFT strain. However, in June, no gulping was performed by the control fish during the behavioral recordings, which may be the result of a decline in their locomotor and agonistic activity. It is probable that, as the active control fish became larger, less oxygen per body weight was available for performing behavioral activity. However, the quieter GIFT fish, required less oxygen, so their lower activity level remained relatively unchanged.

The divergence in locomotor and agonistic behavior of the GIFT and control fish is not surprising, because behavioral traits are among the first traits to respond to domestication; it is usually the frequency or intensity with which a particular behavior is expressed that is affected by domestication (Price 1984). In the Philippines, both fish strains tested were reared under similar hatchery conditions (e.g., pH, salinity, temperature). Thus, the difference in activity level between GIFT and control fish must have been due to a genetic difference between the two types or to pre-fertilization environmental differences (environmental maternal effects) rather than a phenotypic/environmental effect (Swain and Riddell 1990). A genetic basis has been demonstrated for behavioral differences among families (Bakker 1986), populations (Rosenau and McPhail 1987), and closely-related species of fish (Ferguson and Noakes 1982, 1983), but no scientific studies have indicated an effect of the pre-fertilization, maternal environment on behavior (Swain and Riddell 1990). Thus, it is likely that the behavioral differences reported between GIFT and control fish are the result of the selection program described by Pullin (1998) that, by selecting for fast growth, actually selected for calm behavior.

In the comparison of female and male GIFT fish, the growth performance of males was higher than females. The growth advantage experienced by male GIFT fish was connected with a lower activity level. Male GIFT performed less swimming and escaping, and more resting behavior than female GIFT. Even though a higher frequency of agonistic behavior (excluding escape behavior) was exhibited by the fast-growing male GIFT fish, the difference in male and female frequencies was not significant, and the number of bouts of agonistic behavior performed by the male GIFT fish was up to 4.5 times less than male control values. The mirror image stimulation tests supported the finding that male control fish are more aggressive than male GIFT fish. When female and male fish of the GIFT and control strains were compared, the connection between growth and activity level was still observed, suggesting that differences in growth between sexes may be to some extent mediated by behavioral differences. However, in the control fish, the growth rates, and size of male and female fish were similar even though the male control fish performed more swimming and escaping behavior, and less resting than the female control fish. The male controls also exhibited a higher frequency of agonistic activity than the female controls.

In the comparison of female and male fish, low growth of fish was also associated with a high activity level; however, a few experimental observations seemed to deviate from this relationship. For example, the fast-growing male GIFT exhibited a higher frequency of agonistic activity (excluding escape behavior) compared to slow-growing female GIFT, and in the control fish, growth of male and female fish was relatively similar even though, the male control fish performed more locomotor and agonistic acts than the female control fish.

Conventional explanations of the higher growth in males have involved androgens or male sex hormones (Donaldson et al. 1979; Ufodike and Madu 1986). The anabolism-enhancing effect of androgens has been observed in Nile tilapia (Ufodike and Madu 1986), goldfish (Yamazaki 1976), and all salmonids (see Donaldson et al. 1979). Varadaraj and Pandian (1988) suggested, in ‘normal’ (phenotypic and genetic), and phenotypic males Oreochromis mossambicus, that androgens stimulated growth by increasing food intake or food conversion efficiency. Thyroid hormones (T3 and T4) are also involved in controlling growth and development of fish (see Donaldson et al. 1979). Toguyeni et al. (1996, 1997) observed, in the Nile tilapia, that plasma T3 levels were higher in males than females, and thus could account for the males’ growth advantage over females. It was suggested that T3 increases the efficiency of food utilization by males, and thus their growth as well (Toguyeni et al. 1997). Eales and Shostak (1985) also observed, in a population of Arctic char, that plasma T3 levels are strongly correlated with both food ration and growth. However, the behavioral differences, and their effects of oxygen availability for growth provide a more parsimonious explanation for the findings reported here.

Nesting behavior, which is often the first indication of the sexual maturity of fish, was observed only in males. Billy (1982) observed, in Oreochromis mossambicus, a species closely related to Nile tilapia, that both female
and male fish performed nesting behavior, but female fish only performed nesting behavior immediately prior to spawning. Male controls performed more nesting behavior than male GIFT fish. A significantly higher number of nests were also present in the control than GIFT aquaria. Aggression, as observed mostly in the male control fish, appears to be the prevalent mechanism of establishing and maintaining nesting sites (Fenderson et al. 1968; Mabaye 1971; Koebele 1985), and thus attracting mates (Oliveira et al. 1996). The control fish also built more nests earlier in the study (i.e., April) than the GIFT fish; it took the GIFT fish till June to reach the level of nesting activity observed in the control aquaria in April. These findings indicate, at least in males, that the slow-growing control fish became sexually mature sooner, and at a smaller size than the fast-growing GIFT fish. Siddiqui et al. (1997) also observed that in male and female hybrid tilapia, *Oreochromis niloticus* × *O. aureus*, fast-growing fish matured at larger sizes, whereas slow-growing fish matured at smaller sizes. These finding were confirmed by Kolding et al. (2008), who found that in Nile tilapia kept at different dissolved oxygen concentrations, the fish held under low oxygen not only grew more slowly, but also matured at small sizes, as predicted by Pauly (1984).

Size-related mortality was found in both strains of Nile tilapia: dead fish were smaller than the survivors (i.e., live fish). On examination of the bodies of the dead fish, many fish had frayed fins (i.e., pectoral, tail). Christiansen and Jobling (1990), Christiansen et al. (1991), and Siikavuopio et al. (1996) used the incidence of caudal fin damage as an indirect indication of aggressive interactions. If this interpretation is correct, most fish seem to have died from an aggressive encounter with a tank mate or the consequence of the aggression rather than from natural causes. It was suggested that high mortality in small fish may result from starvation as a consequence of the aggression of a few large individuals (Saclauso 1985). This behavior could have elicited inhibitory effects (e.g., small fish become less mobile) which denied the smaller conspecifics access to the food even if it was given in excess (Saclauso 1985).

In the control strain, it was observed that only male control fish experienced size-related mortality. The male control fish could have experienced size-related mortality because they performed more agonistic behavior than females, and the subordinate males, as suggested by Saclauso (1985), were probably unable to evade damaging and potentially lethal attacks of the dominant fish in closely confined aquaria.

Furthermore, control fish suffered a higher mortality than GIFT fish. The higher mortality of control fish could be correlated with their higher bouts of agonistic behavior compared to GIFT fish. Similarly, high mortality rates have been attributed to increase aggressiveness of fish (Saclauso 1985). Siikavuopio et al. (1996) observed a high mortality and incidence of caudal fin damage amongst wild-caught Arctic char, while amongst hatchery-reared fish, mortalities were low and little evidence of fin damage was found. In all, these results add further support to the conclusion that the slow-growing control fish were more aggressive than the fast-growing GIFT fish during the three-month study period.

**Conclusions**

The rearing of cultured fish has become an increasingly important industry. Fish culturists seek fish strains that possess high growth rates and reach harvestable size before attaining sexual maturation. Sexual maturation of fish can complicate production operations and/or affect product quality. This is especially important for the tilapia which, when they mature precociously, can overpopulate waters with small, stunted fish. Aggressiveness in the form of attacking and fin-nipping, also associated with breeding behavior, is an undesirable habit for farmed fish (Balarin and Hatton 1979) and one for important consideration when choosing a tilapiine strain for culture practices. It has been argued that in competitive environments, artificial selection for fast growth may lead to higher levels of overall aggression, and therefore would result in no net gain in assimilation efficiency or growth in the populations (Kinghorn 1983).

However, considering the oxygen demand of various behaviors of fish under domestication, such as in Nile tilapia, could be used in their selective breeding. The results of behavioral studies are likely to be of more direct utility to breeders than most physiological and biochemical measures such as food conversion efficiency, and protein, lipid and water contents of body tissues, which are indirect results of the underlying scarcity of oxygen available for growth in fish exhibiting, e.g., aggressive, oxygen-demanding behaviors (Pauly 1981, 2010).
The main focus of many breeders is on genetic improvement of farmed fish. If indeed quiet behavior reflects an underlying genetic variation and thus amenable to selection (as the GIFT fish demonstrate), then it could be incorporated into or even become the primary criterion of fish breeding programs. Quiet behavior could also be correlated with other desirable traits (e.g., high survival, disease resistance). The domestication of livestock (notably cattle) has involved a similar selection strategy.

**ACKNOWLEDGEMENTS**

We thank the International Center for Living Aquatic Resources Management (ICLARM) for donating the two strains of Nile tilapia used in this study. We also like to thank everyone from the UBC Zoology Department workshop, especially Professor Robin Liley for his guidance and Mr. Bruce Gillespie, for providing technical assistance. Daniel Pauly wants to acknowledge the immense contribution of R.S.V. Pullin in leading the development of the GIFT strain of Nile tilapia, and for many years of collaboration and friendship.

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