A COMPARISON OF THE SWIMMING PERFORMANCE BETWEEN TRANSGENIC AND NORMAL COHO SALMON (*ONCORHYNCHUS KISUTCH)*

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Abstract

We have examined the consequence of remarkably fast growth rates in transgenic fish as a physiological fitness variable. Substantially faster growth rates were achieved by the insertion of an "all-salmon" growth hormone gene construct in transgenic coho salmon. On an absolute basis, transgenic fish swam no faster at their critical swimming speed than smaller, non-transgenic controls, and relative to older, non-transgenic controls of the same size, the transgenic fish swam much slower. Thus, we find a marked trade off between growth rate and swimming performance. These results suggest that transgenic fish may be an excellent model to evaluate existing ideas regarding physiological design.

Introduction

Transgenic technologies have advanced to such a degree that considerable concern exists about the possibility of escapement of transgenic fish (Kapuscinski and Hallerman, 1991; Devlin and Donaldson, 1992). This concern centres around the possibility that transgenic fish could outcompete "wild" fish, if, for example, growth-enhanced fish were to consume food resources more efficiently or possess enhanced physiological capacity due to increased size or strength. Nevertheless, we are not aware of any assessment of the physiological fitness of transgenic fish. One reason for the lack of such studies is the scarcity and expense of transgenic fish. In the present study, we took advantage of a limited supply of transgenic coho salmon containing an "all-salmon" growth hormone gene construct (OnMTGH1). This gene construct increases the growth of coho salmon by an average 11-fold compared with non-transgenic controls (Devlin *et al*. 1994).

By comparing the critical swimming speeds of transgenic and non-transgenic control fish, we tested the hypothesis that the growth-stimulated transgenic fish would be faster swimmers. The rationale for this hypothesis was the well known fact that the absolute swimming speed (cm/s) of salmon increases with body length (Brett 1971, 1975; Beamish 1978).

Materials and Methods

Animals

Three groups of fish were studied. Transgenic coho salmon (N=6) were produced by microinjection of OnMTGH1 into fertilized eggs (Devlin et al. 1994). They were raised for one year at the West Vancouver Fisheries and Oceans laboratories in fresh wellwater at 10 ± 1^0 C and fed a commercial salmon diet *ad libitum*. Non-transgenic fish were raised under the same conditions and were either of the same year class (N=6) and smaller, or one year older (N=6) and of similar size as the transgenic fish.

Swimming Performance

We compared the swimming performance of transgenic and non-transgenic fish using a standard measure, the critical swimming speed (U_{crit}), and standard techniques (Beamish 1978; Farrell *et al* 1991). We selected U_{crit} as the performance measure because salmon swimming at U_{crit} are thought to be at or close to their maximum oxygen consumption and cardiac output (Thorarensen *et al*. 1996). The U_{crit} measurements were made with a water-jacketed swim chamber with inside dimensions of 24.0 cm x 15.5 cm x 24.5 cm. The propeller was driven by a permanent magnet D.C. motor and controlled via rheostat and tachometer. Waster velocity was calibrated with a Swoffer instrument model 2100 series current velocity meter (Seattle, Wa.). Freshwater was supplied to the inner swim chamber at a rate of 1.5 L/min and allowed to flow into the outer jacket where it was directed to the outflow drain. Dissolved oxygen varied between 8.0 mg/L and 10.4 mg/L as measured by an oxygen electrode (Oxyguard, Vancouver, B.C.) while temperature varied between 11^0 C and 13^0 C. Each fish was introduced into the swim chamber for 4 h to 12 h before the swimming tests were performed and allowed to habituate to a water flow rate of approximately 0.5 body lengths per second (bl/s) during this period. To measure U_{crit}, the water velocity was increased in increments of 5 cm/s every 20 min until the fish fatigued. Upon fatigue the experiment was terminated and the fish were allowed to recover for 40 min, anaesthetized with buffered MS 222 (100 ppm) and then weighed, measured and adiposed clipped. The adipose clip prevented the same fish being tested twice once returned to the holding tank after regaining consciousness. U_{crit} values were calculated according to the methods of Bell and Terhune (1971) with appropriate corrections, if necessary, for the blocking effect. All values are presented as means and SEM.

Results

Growth enhanced transgenic fish were more than twice as long (22.0 ± 1.24 *vs* 9.6 ± 0.17 cm) and more than 10-fold heavier (121.6 ± 8.4 g *vs* 11.0 ± 0.25 g) compared with the non-transgenic controls of the same year class. Despite this larger size, the absolute critical swimming speed of the transgenic fish was not statistically different ($P>0.05$, Students t-test) to that of the non-transgenics (Fig. 1). Both groups of fish had a U_{crit} value of around 47 cm/s.

In contrast, non-transgenic control fish that had one extra year to grow to approximately the same size (20.1 ± 0.14 cm) and weight (86.1 ± 7.8 g) as the younger transgenics swam significantly faster ($p<0.05$, Student t-test) than the transgenic fish (Fig. 1). Thus, our dasta indicate that these growth- enhanced transgenic coho salmon do not swim at speeds comparable to wild-type fish of approximately the same size.

Discussion

Our data for control fish fit well within the extablished range of U_{crit} for similar-sized non-transgenic juvenile coho salmon and sockeye salmon (Fig. 1). Thus, we have confidence in differences in U_{crit} and conclude that transgenic salmon are capable of swimming at speeds only about half of what would be predicted based on body size alone. In fact, it appears as if the transgenic fish retain a "juvenile" level of swimming performance since they swam at essentially the same speed as smaller fish from the same year class. It is possible to speculate that the poorer swimming performance of these growth-enhanced transgenic fish arises either from an ontogenetic delay, or from disruption of the locomotory muscles and/or their associated support systems (e.g., respiratory, circulatory systems and nnotervous systems). We have also observed abnormalities in growth-enhanced fish (Devlin *et al.* 1995), particularly with opercular morphology, which might contribute to the poorer swimming performance. However, further work is needed to resolve this matter. Furthermore, since there is usually a range of growth enhancement both within and among transgenic groups, future work must resolve whether or not other strains or species of growth-enhanced fish show as marked a decrease in swimming performance as in the present study.

Even though these transgenic fish show a "suppressed" swimming performance, other physiological processes were obviously not limited in the same way. The digestive system, for example, was functioning efficiently, otherwise the more than 10-fold difference in body size would not be possible. We know that appetite is increased, but have no information about the absorptive processes that occur in the digestive tract. These transgenic salmon also appear to display early smoltification (the osmoregulatory adaptation to marine conditions) (B. Devlin and C.Clarke, unpubl. obs.). Collectively, these observations raise the possibility that the heightened ability of transgenic fish in some physiological processes occurs at the expense of the locomotory system, and perhaps other physiological systems as well. If this proves to be the case, we may need to revise our ideas on symmorphosis (Weibel, Taylor and Hoppeler, 1991) and safey factors (Diamond and Hammond, 1992) in a design of physiological systems and in resource budgeting in fish. This information may also be of value when estimating the risks associated with escapement of growth-enhanced transgenic fish. Our results clearly show that bigger is not exclusively better for all physiological functions.

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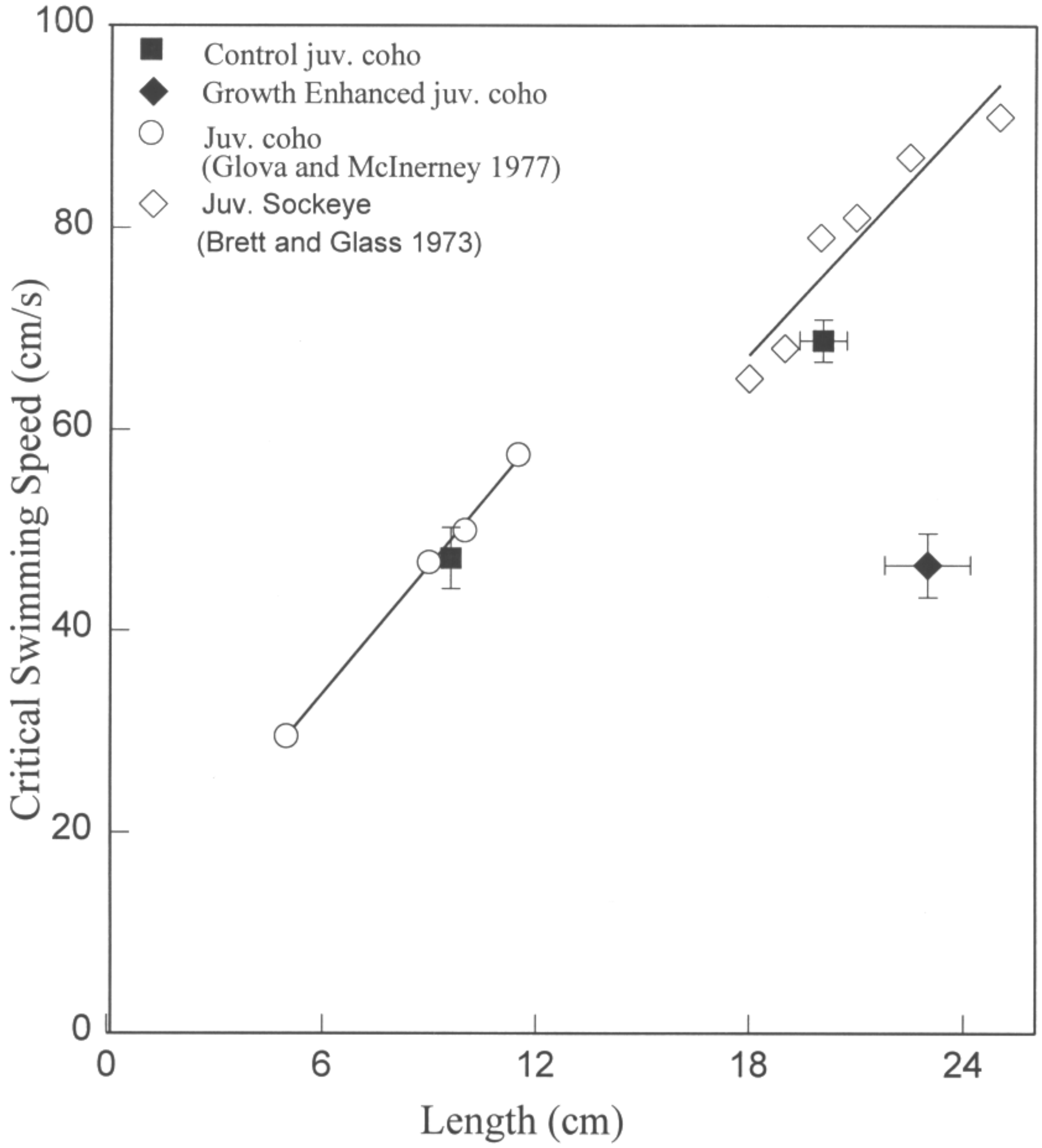
FIGURE. 1 A comparison of the absolute critical swimming speed of juvenile salmon as a function of body length. Our data for control coho (solid squares) illustrate that as juvenile salmon increase in length, they increase their absolute swimming speed. Our data also fall within the established ranges for the swimming performance of juvenile coho (open circles; Glova and McInerney 1977) and sockeye (open diamonds; Brett and Glass 1973) salmon under comparable environmental conditions (data were selected for freshwater at 10^{0} C). In contrast, the swimming performance of transgenic coho (solid diamonds) is significantly below that of similarly-sized coho and sockeye salmon.

Fig. 1


Control juv. coho
Growth Enhanced juv. coho
Juv. coho
(Glova and McInerney 1977)
Juv. Sockeye
(Brett and Glass 1973)
Critical Swimming Speed (cm/s)
Length (cm)
0
20
40
60
80
100
0
6
12
18
24

6

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