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Swimming performance of the European minnow

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Maximum sustained swimming speeds of the European minnow were examined using increased velocity tests in a swim-speed chamber. Maximum sustained swimming speed for the size class 50–64 mm was 10.4 ± 4.0 cm s^{-1} (mean ± SD), for the size class 65–79 mm 14.2 ± 4.8 cm s^{-1}, and for the size class 80–105 mm 16.0 ± 5.6 cm s^{-1}. Similarly sized minnows were able to maintain considerably higher speeds in a raceway. For instance, individuals of the largest size class could maintain a swimming speed of 34 cm s^{-1} for at least 25 min. Hence, the maximum swimming capacity of the fish was highly underestimated using the increased velocity test in the swim-speed chamber. The unintentional distribution of minnows by man to new watersheds is considered a critical environmental problem in Norway, because of their potential to develop high densities in communities with low diversity. Recorded high swimming speeds indicated minnows' capability to spread further upstream when introduced to new water systems, and that their swimming and jumping abilities must be taken into account when constructing migration barriers to prevent further spreading. High swimming speeds could also indicate minnows' potential for competing with salmonids not only in lakes but also in riverine environments.

Introduction

The natural distribution of the European minnow (*Phoxinus phoxinus*) in Norway was mainly restricted to low-altitude localities in the south-eastern part of the country. The distribution area expanded considerably throughout the 1900s, mainly as a result of the use of minnows as live bait for angling. As a result, the European minnow is fast becoming the most widely ranging fish species in Norwegian rivers and lakes (Hesthagen and Sandlund 2004, Museth *et al.* 2007). This unintentional distribution of bait fish is considered a critical environmental problem by the management authorities. Bait species can achieve very high densities when introduced to communities with low fish species diversity, such as in numerous lakes where brown trout is the only fish species present. In lakes where dense minnow populations have been found, an average 35% reduction in brown trout abundance, along with concurrent reductions in recruitment and growth rates, have been observed (Museth *et al.* 2007). Only very few detailed analyses

of the interactions between brown trout and the European minnow exist, and the underlying mechanisms for the negative impacts are not understood. Bait species have also been recently introduced to several river catchments with important Atlantic salmon (*Salmo salar*) and sea trout (*Salmo trutta*) populations (Museth *et al*. 2007). The potential impact of minnow on Atlantic salmon and sea trout populations is not known, but there is concern that these populations may also be negatively affected.

Swimming performance is one of the important components of fish survival as it relates to the capacity to maintain station against currents, avoid predators and acquire food, thus making swimming performance a potential fitness parameter, and a matter of physiological and ecological interest (Beamish 1978, Plaut 2001). Information on swimming performance of the European minnow may be important in understanding and predicting the negative impacts on native salmonids in different habitats. Furthermore, knowledge on swimming performance is of great importance when assessing the risk of introductions into water systems. Swimming performance knowledge can also be important when constructing artificial barriers to reduce the dispersal of the European minnow in waterways (Holthe *et al*. 2005).

The primary aim of our study was to examine critical swimming speeds of the European minnow using increased velocity tests in a swim-speed chamber. An increased velocity test in a swim-speed chamber is a commonly used method to investigate the maximum sustained swimming speed of fish (Brett 1964, 1967, Farlinger and Beamish 1977, Beamish 1978, Jain *et al*. 1997, Ytrestøyl *et al*. 2001). However, conditions in a swim-speed chamber may differ from swimming experiences of free ranging fish (Plaut 2001). We, therefore, also compared the results with observations from a raceway.

Material and methods

The minnows were captured at Røros, central Norway (62°35´N, 11°20´E), using fish traps and moved to a cage for 12-h acclimation. The duration of the acclimation period was chosen as a compromise between letting the fish recover from the immediate stress response of capture, but without introducing the long-term stress from being held in captivity. The European minnow is a well suited species for such studies, as they seem to tolerate capture and handling stress much better than for instance salmonids (own observations). Individuals were maintained at velocities they had previously acclimated to prior to capture. None of the fish showed signs of damage after capture and transportation. The minnows were divided into tree size classes (total length); 1: 50–64 mm, 2: 65–79 mm, and 3: 80–105 mm. Fifteen individuals from each size class were used for each swim experiment in the swim-speed chamber and the raceway (n_{total} = 90). Maximum sustained swimming speed was determined using an increased velocity test in the swim-speed chamber (Fig. 1; Beamish 1978). An artificial stream in the raceway (Fig. 2) was subsequently used to monitor data on swimming performance using fixed velocity tests. Both experiments were conducted during 4–24 July 2001. Water temperatures in the swim-speed chamber were in the range 13.7–16.6 °C and in the raceway 12.7–14.2 °C, both similar to temperatures in the cage and in the river where the fish were captured.

Experimental trials in the swim speed chamber

The Blazka type swim-speed chamber was a tube-within-a-tube design (Fig. 1, for further description, *see* Booth *et al*. 1997). Total volume of the swim-speed chamber was four litres. The water speed ranged from 0–42 cm s^{-1} and was adjusted using a calibrating curve. Any blocking effect from the fish was excluded due to a small cross-section area of the fish as compared with the cross-section area of the tube itself (Smit *et al*. 1971). Water is the swim-speed chamber was well aerated (water exchange rate of 1.5 l min^{-1}; Fig. 1).

The fish were acclimated for two hours in the swim-speed chamber without any current but with continuous exchange of fresh water. The fish were then exposed to an initial current of 1.5 cm s^{-1}, which was then inreased by

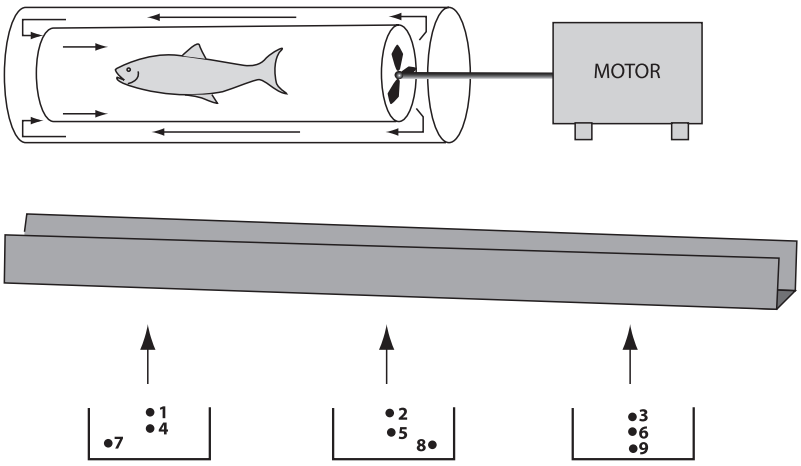

Fig. 1. Top: Illustration of the swim-speed chamber used for swim tests. Arrows indicate the direction of the water flow. Bottom: The raceway used for swim tests (l × w × d: 4.2 × 0.4 × 0.25 m). Underneath, the measuring points of the water current. The uppermost measuring point was 1 and the lowermost measuring point 9 in the current direction.

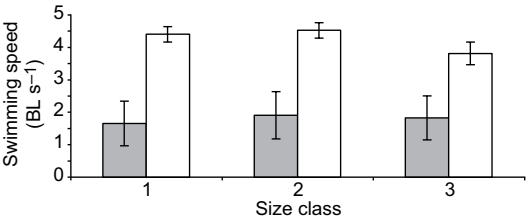

Fig. 2. Maximum mean swimming speeds in body lengths per second (BL s^{-1} ± SD) for the three size classes of the European minnow (class 1 = 50–64 mm total body length, class 2 = 65–79 mm, and class 3 = 80–105 mm). White bars represent mean swimming speeds (± SD) recorded in the raceway, and grey bars represent the mean maximum sustained swimming speeds (± SD) recorded in the swim chamber. Each bar represents data from 15 individuals (n_{total} = 90).

3.5 cm s^{-1} every five minutes. The fish were considered fatigued when they could no longer maintain position and were impinged on the downstream screen. At this speed, the fish had reached the maximum sustained swimming speed. After the fish was considered fatigued it was given five minutes to recover, and water velocity was directly raised to the maximum sustained swimming speed. None of the fish were able to swim at any higher velocities after this.

Experimental trials in the raceway

An artificial stream was constructed from a fiberglass raceway (Fig. 2). Two tubes supplied the raceway with water at 12.5 l s^{-1}, which resulted in a water depth of 10 cm. Water velocities were adjusted by changing the level of the raceway. Water velocities were measured with a Schiltknecht Mini Air 2 propeller-based current measuring instrument at nine points (Fig. 1) for six seconds and a mean value was calculated. Since tested minnows typically chose areas in the raceway with the lowest water velocities, a mean velocity of three points was used in the statistical analyses of the data (points 7, 8 and 9) (Fig. 1).

During swim trials, water velocity was about two times higher than the mean maximum sustained swimming speed for each size class in the swim-speed chamber. This was done because pilot tests indicated that the minnows could maintain higher speeds in the raceway than in the swim-speed chamber. The fish were considered fatigued when they had swum for the same time as the mean time for the size class in the swim-speed chamber, even if the fish did not show signs of exhaustion. This was done to have a comparable basis for the physiological samples between the two test protocols. The time interval for size class one was 15 min, for size class two 20 min and for size class three 25 min. The fish were acclimated in cages at the location and transferred to the raceway with a net.

Blood samples

Blood samples were collected from unexercised and exercised fish by cutting a tail, and drawing one drop of blood which was then trans-

ferred onto two test strips (it was not possible to obtain enough blood from the caudal vessel using syringes). The test strips were analysed *in situ* with a Lactate Pro instrument (Arkay, KDK Corporation, Kyoto, Japan), and a MediSense Precision Plus glucose instrument (Abott laboratories, Bedford, USA). Blood samples were collected from all fish instantly after exercise. Control samples were taken from three fish from each size class at capture, and after 12 hours of acclimatisation in the cage. Control samples were taken both for the trials in the swim-speed chamber and in the raceway. Experiments in the swim-speed chamber and the raceway were done during slightly different periods (4–15 July 2001 and 13–24 July, respectively) and at slightly different water temperatures (13.7–16.6 °C and 11.7–14.2 °C, respectively). The control groups were, therefore, kept separately. Fish were not anaesthetized but killed by a blow to the head before the tail cutting procedure to avoid any interaction between anaesthetic and lactate elevation in fish (Iversen *et al*. 2003).

Results

Experimental trials in the swim speed chamber

The mean (± SD) maximum sustained swimming speed for the minnows was 1.79 ± 0.6 body lengths (BL) s^{-1} (13.9 ± 5.3 cm s^{-1}), and the highest speed registered was 3.8 BL s^{-1} (33.0 cm s^{-1}) for a fish of 88 mm body length. The mean relative swimming speeds for the three size classes were: size class one 1.64 ± 0.6 BL s^{-1}, size class two 1.91 ± 0.7 BL s^{-1} and size class three 1.81 ± 0.6 BL s^{-1} (10.4 ± 4.0 cm s^{-1}, 14.2 ± 4.8 cm s^{-1} and 16.0 ± 5.6 cm s^{-1}, respectively) (Fig. 2).

Blood parameters of unexercised fish at capture (n = 9) and 12 h after capture (n = 9) were not significantly different (independent samples t-test: $p_{lactate}$ = 0.22, $p_{glucose}$ = 0.67) and as a result data from these two groups were pooled. The lactate blood plasma level (mean ± SD) was higher for exercised (n = 45, 10.12 ± 3.23 mmol l^{-1}) than for unexercised fish (n = 18, 7.06 ± 1.85 mmol l^{-1}) (independent samples t-test: $p < 0.001$). The fish achieving the higher relative swimming speeds did not have a higher accumulation of blood lactate than the fish achieving lower speeds (linear regression: p = 0.96, r^2 = 0.22). There was no significant difference in the mean (± SD) plasma glucose level in unexercised (n = 18, 3.96 ± 1.50 mmol l^{-1}) and exercised fish (n = 45, 4.87 ± 2.64 mmol l^{-1}) (independent samples t-test: p = 0.068).

Experimental trials in the raceway

Fishes of the three size classes were tested in the raceway at different water velocities; size class one was tested at 26 cm s^{-1}, size class two at 32 cm s^{-1} and size class three at 34 cm s^{-1} (4.40 ± 0.24 BL s^{-1}, 4.52 ± 0.24 BL s^{-1} and 3.81 ± 0.35 BL s^{-1}, respectively) (Fig. 2). The mean water velocity was 31 cm s^{-1} (4.25 BL s^{-1}) for the three size classes combined. The highest relative swimming speed was 4.97 BL s^{-1} for a fish of 53 mm body length.

Also in the raceway experiment, the blood parameters of unexercised fish at capture (n = 9) and 12 h after capture (n = 9) were not significantly different (independent samples t-test: $p_{lactate}$ = 0.22, $p_{glucose}$ = 0.67), and data from these two groups were pooled. The lactate blood plasma level (mean ± SD) was higher in exercised (n = 45, 9.49 ± 1.86 mmol l^{-1}) than in unexercised fish (n = 18, 6.99 ± 3.17 mmol l^{-1} (independent samples t-test: p = 0.001). As compared with fish swimming at the lower relative speeds, the fish swimming at the highest relative speeds did not show any sign of higher accumulation of blood lactate (linear regression: p = 0.070, r^2 = 0.047). There was no difference in the plasma glucose level (mean ± SD) between unexercised (n = 18, 3.96 ± 1.50 mmol l^{-1}) and exercised fish (n = 45, 4.40 ± 2.07 mmol l^{-1} (independent samples t-test: p = 0.35).

Discussion

This study demonstrated that European minnows are capable of obtaining and maintaining relatively high swimming speeds, with mean maximum sustained swimming speed of 16 cm s^{-1} for the largest size group. In the raceway, individuals

of the largest size group could maintain a swimming speed of 34 cm s^{-1} for at least 25 minutes. This means that European minnows are capable of invading new upstream areas of water systems through stretches of relatively fast-flowing water, with the largest individuals having the largest spreading capacity against currents. The capacity to move upstream is likely dependent on the length of stretches with continuously fast-flowing water, and on the frequency of pools. Pools offer resting possibilities, and may facilitate upstream migration in otherwise fast-flowing areas. A previous study demonstrated that minnows are able to negotiate waterfall barriers up to 27 cm high (Holthe *et al*. 2005), further emphasising their strong spreading capabilities. Jumping abilities of minnows are highly reduced at low water temperatures (5–7 °C, Holthe *et al*. 2005). It is, therefore, likely that also maximum swimming speeds and, therefore, the risk of distribution, are highly reduced at such low water temperatures, as shown for many other fish species (Kieffer 2000). This hypothesis was confirmed by trials in the raceway at 5.8 °C and 34 cm s^{-1}, where no minnows were able to withstand the current at all (own unpubl. data). Hence, upstream spreading of minnows is more likely at summer than winter temperatures, and barriers constructed to prevent dispersal of minnows are more critical in the summer than mid-winter.

The European minnow had lower maximum sustained swimming speeds than demonstrated for Atlantic salmon juveniles in a similar, but not directly comparable, laboratory study (McDonald *et al*. 1998). However, the ability to maintain relatively high swimming speeds emphasises the potential of European minnows to compete with salmonids not only in lakes and slow flowing waters, but also with the Atlantic salmon and brown trout in river environments. The European minnow do not appear to be a strong competitor in the relatively complex fish communities of its native range, unlike many rivers in Norway, which are typically characterised by low fish species diversity, with few species other than the Atlantic salmon and brown trout (Museth *et al*. 2007). The sympatric Atlantic salmon and brown trout differ slightly in their habitat use, with the Atlantic salmon preferring elevated water velocities (mean water column velocity up to 80 cm s^{-1} and microhabitat velocity of 3–25 cm s^{-1} for parr > 7 cm) and brown trout moderate-to-low water velocities (Heggenes *et al*. 1999). Based on the results in the present study, it seems like the largest minnows with the strongest swimming capabilities have a larger potential to compete with the Atlantic salmon than the smaller minnows. All of the tested size groups have the potential to compete with brown trout, based on the slower flow preferred by this species. However, the outcome of interspecific competition among the European minnow and these anadromous salmonids are likely influenced by a number of parameters such as body size, habitat use, diet, predation and fish densities. Further work is required to examine the interactions of these factors and their influence on the ability of minnows to invade new territory.

Minnows in the raceway maintained considerably higher swimming speeds than fish in the swim-speed chamber, indicating that higher maximum swimming speeds could be obtained in the raceway than in the swim-speed chamber. However, all fish had a significant congestion of lactate in the blood, which implies that the fish were fatigued under both test protocols (Iwama *et al*. 1997). Lactate is a waste product that accumulates in the muscle during exercise when glycogen changes into ATP under anaerobic conditions (Driedzic and Hochachka 1978). Lactate is transported from the muscle and into the blood stream, and the lactate concentrations in the blood can therefore be used as an indicator of fatigue.

Some of the differences in the recorded swimming speeds between the swim-speed chamber and the raceway could possibly be due to the fact that the minnows used the turbulence formed in the raceway. However, by measuring the velocity over a time interval of six seconds, the turbulence was included in the actual velocity measurements. A propeller-based current measuring instrument probably underestimates the water velocity by 2–3 cm s^{-1} as compared with an acoustical Doppler current measuring instrument (ADP) (Golmen and Sundfjord 1999), which suggests that in the present study the water current in the raceway was actually higher than measured, and that the differences in swimming speeds between the methods were underestimated.

In this study, a 3.5 cm s^{-1} current velocity increment every five minutes was used to measure the maximum sustained swimming speed of minnows. However, the magnitude of the velocity increments and the time interval between increments vary among studies of critical swim speeds. Brett (1964, 1967) recommended a time interval of 60 min since shorter intervals could result in unrealistically high critical swimming speeds. On the other hand, Beamish (1980) found no significant variation in critical swimming speeds using time intervals of 5, 10 and 75 min and velocity increments of 5 and 10 cm s^{-1} in a study of the Arctic char (*Salvelinus alpinus*). Hunter and Scherer (1988) found in another study of the Artic char that there was no significant difference in critical swimming speeds using time intervals of 15 and 75 min with velocity increments of 10 cm s^{-1}. For small fish as the European minnows, smaller velocity increments and a short time interval had to be used, and such differences among studies often makes it difficult to directly compare the results.

The advantage of the fixed velocity test as compared with the increased velocity tests is that the fish is exhausted under stable physiological conditions (Hammer 1995). Webb (1971a, 1971b) reported that after an increase in velocity fish responded with a period of irregular swimming, and used certain time to adjust to the new demands for cardiovascular and ventilatory activity. These results implied that during first minutes after an increase in velocity, the fish used anaerobic energy pathways (Webb 1971a, 1971b). This energy fraction is accumulative and the acid-base relations change towards a metabolic acidosis (Brett 1964, Hammer 1995), which may lead to a shorter fatigue time. This is probably the physiological reason why the use of the increased velocity test can underestimate the true swimming capacity of fish. The artificial setting in the swim-speed chamber, as compared to the more natural conditions in the raceway, may also add more stress or reduce the motivation of the fish to swim. We conclude that the commonly used increased velocity tests in a swim-speed chamber may considerably underestimate the true maximum swimming capacity, and should therefore be used with care when aiming at recording swimming capacities representative for natural conditions. Both methods used in the present study must be regarded as forced swim trials, and the European minnow may likely obtain even higher swim speeds during spontaneous activity under natural or semi-natural conditions. Hence, even though high swimming speeds were recorded for minnow in this study, we assume that maximum swimming capacity under natural conditions is even higher. It is also reasonable to expect that wild fish are to some extent stressed by being captured and by the experimental situation. Acute stress may lead to impaired swimming performance (Wedemeyer and McLeay 1981), and also for this reason we assume that the maximum swimming capacity under natural conditions is higher.

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