# Swimming Speeds in Fish: phase 2 Literature Review

ENVIRONMENT
AGENCY

The Environment Agency is the leading public body protecting and improving the environment in England and Wales.

It's our job to make sure that air, land and water are looked after by everyone in today's society, so that tomorrow's generations inherit a cleaner, healthier world.

Our work includes tackling flooding and pollution incidents, reducing industry's impacts on the environment, cleaning up rivers, coastal waters and contaminated land, and improving wildlife habitats.

This report is the result of research commissioned and funded by the Environment Agency's Science Programme.

**Author(s):**
Clough, S.C., Lee-Elliott, I.E., Turnpenny, A.W.H., Holden, S.D.J., and Hinks, C.

# Science at the Environment Agency

Science underpins the work of the Environment Agency, by providing an up to date understanding of the world about us, and helping us to develop monitoring tools and techniques to manage our environment as efficiently as possible.

The work of the Science Group is a key ingredient in the partnership between research, policy and operations that enables the Agency to protect and restore our environment.

The Environment Agency's Science Group focuses on five main areas of activity:

- **Setting the agenda**: To identify the strategic science needs of the Agency to inform its advisory and regulatory roles.
- **Sponsoring science**: To fund people and projects in response to the needs identified by the agenda setting.
- **Managing science**: To ensure that each project we fund is fit for purpose and that it is executed according to international scientific standards.
- **Carrying out science**: To undertake the research itself, by those best placed to do it - either by in-house Agency scientists, or by contracting it out to universities, research institutes or consultancies.
- **Providing advice**: To ensure that the knowledge, tools and techniques generated by the science programme are taken up by relevant decision-makers, policy makers and operational staff.

Professor Mike Depledge          Head of Science

# CONTENTS

# 1.    INTRODUCTION

## 1.1    Background

The study of fish swimming speeds is relevant to many aspects of fisheries and fish conservation, notably fishing gear design and operation, prevention of fish entrainment at water intakes and fish pass design. Interest in these and other applications, combined with academic curiosity, has led to investigations spanning more than a century into every aspect of fish swimming. The subjects of study have included ichthyomechanics, physiology, biochemistry, energetics and ecological implications. A review of the literature for the purposes of Phase 1 of the present study identified several hundred scientific reports and papers relating to fish swimming speed.

The review presented during Phase 1 was focused on the following key freshwater species:

| | |
|---|---|
| brown trout | *Salmo trutta* L. |
| chub | *Leuciscus cephalus* (L.) |
| dace | *Leuciscus leuciscus* (L.) |
| roach | *Rutilus rutilus* (L.) |
| elver | *Anguilla anguilla* (L.) |

Supplementary species of interest were:

| | |
|---|---|
| barbel | *Barbus barbus* (L.) |
| perch | *Perca fluviatilis* L. |
| pike | *Esox lucius* L. |

For Phase 2, the review presented here is focused on the following key freshwater species, selected for immediate laboratory investigation:

| | |
|---|---|
| grayling | *Thymallus thymallus* (L.) |
| eel | *Anguilla anguilla* (L.) |
| barbel | *Barbus barbus* (L.) |
| bream | *Abramis brama* (L.) |

Supplementary species of interest, which may be selected for testing later in the laboratory programme are:

| | |
|---|---|
| perch | *Perca fluviatilis* L. |
| pike | *Esox lucius* L. |
| stone loach | *Barbatula barbatula* (L.) |
| bullhead | *Cottus gobio* L. |
| river lamprey | *Lampetra fluviatilis* |
| twaite shad | *Alosa fallax* (Lacepede) |

The first review was intended to provide a general briefing on a number of topics that underpin the science of fish swimming performance, and then to collate and critically review available swimming performance data on the selected species.

The purpose of the present review is to collate and critically review available swimming performance data on the species selected for Phase 2 of the study, and the supplementary species of interest. Reference to other closely related species will be made where this is necessary to illustrate a technical point, however to avoid extensive repetition the physiological background to fish swimming provided in the first review will be omitted. Relevant general information published since the first review will also be referenced where appropriate.

## 1.2 Brief summary of factors influencing fish swimming performance

A number of variables influence the swimming performance within a given species, in particular fish size and water-temperature (Bergman, 1987). There also exists a (sometimes substantial) degree of inter-individual variation resulting from differences in genetic make-up, health and condition. Biological factors including parasite loading (Wagner *et al.,* 2003) and the presence or absence of skin mucus (Sagnes *et al*., 2000) are likely to influence swimming performance, and chemical factors such as dissolved oxygen concentration (Domenici *et al.,* 2000), acidity (Neuman, 1979) and the presence of pollutants such as tri-N-butyltin chloride (Ylae-Mononen, 1989) and aluminium (Ytrestoyl *et al*., 2001) can also be important. For shoaling species, the position within the shoal is also known to affect swimming performance (Svendsen *et al.,* 2003). When considering the movement of fish through fish passage facilities factors such as turbulence and air entrainment may be important, as well as the water velocity (Haro *et al*., 1999).

Important considerations when interpreting published data are the handling and experimental methodologies used to determine swimming performance. Poor handling techniques or disease may cause stress to fish, leading to under-performance in trials, and some methodologies may not stretch the fish sufficiently to yield maximum performance information. Equally, lack of rigour in fully reporting the experimental conditions, especially temperatures at which measurements were made, may compromise the value of otherwise sound data.

Studies of fish migration using techniques such as radio-telemetry, mark-recapture and more recently hydroacoustics (Pedersen, 2001) can provide important information not only on the mobility of fish species, but also on the speed at which fish naturally move around their environment. Where available, such data will be included in the review, but can not be used as indicators of maximum performance, as fish rarely swim at the peak of their ability.

## 2. SPECIES OF INTEREST

### 2.1 Grayling (Thymallus thymallus)

#### 2.1.1 Background

The European grayling (*Thymallus thymallus*) is known to be migratory, and can be classed as potamodromous. Jungwirth (1996) demonstrated that from an estimated population of 13,300 adult grayling downstream of a nature like bypass channel, 17% migrated through the pass. Evidence suggests that European grayling are comparatively poor at passing around obstacles such as dams (Northcote, 1995; Persat, 1996) although it is not clear whether this is the function of a low burst swimming ability. As drift feeders grayling spend extended periods in shallow fast flowing water at the downstream ends of pools (S. Clough, pers. obs.). Their streamlined body shape is well designed to resisting flow, and considering their habitat choice and feeding mode it is perhaps reasonable to expect a high level of performance in endurance trials.

#### 2.1.2 Swimming speeds

Few studies have examined the swimming speeds of the European grayling (*Thymallus thymallus*), and there is conflicting evidence within the literature regarding the swimming ability of members of the genus *Thymallus*. Northcote (1998) describes the graylings as being weak swimmers that have difficulties in even moderate flows. Conversely, Stolvov & Alikin (1977) discussed the influence of temperature on oxygen consumption in *T. arcticus* at rest and at different swimming speeds, and concluded that this species is adapted to active swimming at high speeds. The apparent discrepancy between morphological characteristics and observed performance may reflect problems with underachievement in laboratory or field trials. Northcote (1998) states that the sustained swimming of many fish can be described by the formula $V = KL^e$, where V is velocity in cm s$^{-1}$, K is constant, L is the fish's length in cm and *e* another constant. For Arctic grayling (*T. arcticus*), K = 36 and *e* = 0.19. Using this formula, the sustained swimming speed of a 25 cm fish would be around 66 cm s$^{-1}$ (Figure 1);
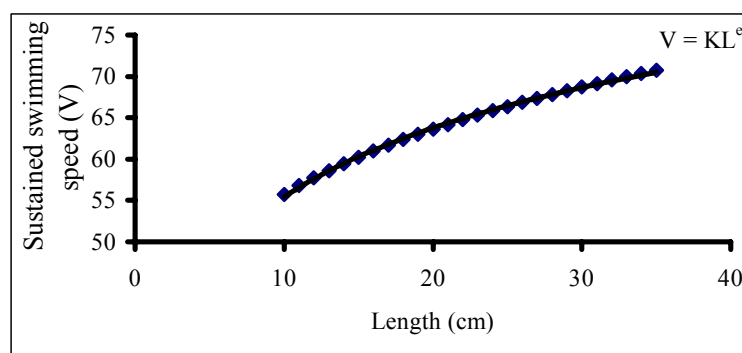


Figure 1. Sustained swimming of Arctic grayling derived from the formula given by Northcote (1998).

#### 2.1.3 Other aspects of swimming

The following papers refer to aspects of swimming in members of the genus *Thymallus*. These and equivalent references for the other fish groups covered in this review have

been included for general interest and because they may have some relevance in later interpretation of the laboratory findings.

Sagnes *et al*. (2000) found that the drag coefficient of grayling *T. thymallus* was dependent on body surface conditions and rigidity, and that the presence of skin mucus on fish could reduce drag coefficient by 10%. The authors also suggested that grayling morphology evolves towards hydrodynamically efficient shape at high velocities, and there is a relationship between these shifts in hydrodynamic abilities and the different habitats (in terms of current velocity) used by five morphological groups.

Hughes & Kelly (1996) describe a hydrodynamic model for estimating the energetic cost of swimming manoeuvres of Arctic grayling (*Thymallus arcticus*). Matyukhin *et al*., (1973) examined the swimming efficiency of the Lake Baikal grayling (*Thymallus arcticus baicalensis*) under various speeds in a 'biohydrodynamic' unit, and showed that the highest efficiency was observed at swimming speeds of 77 to 87 cm per second. Matyukhin & D'yachenko (1976) demonstrated that there was a change in the values of an electromyogram (EMG) of the red and white muscles in different parts of the body of the Baikal grayling, (*T. arcticus baicalensis*), when studied at controlled swimming speeds (37, 57, 77 and 87 cm per sec) in an experimental apparatus. At lower speeds of swimming the mean electrical activity is greater in the red muscles than in the white muscles. An increase in electrical activity in the red muscles is observed up to the swimming speed of 77 cm s$^{-1}$ but thereafter it decreases or ceases altogether. An intensive increase in EMG values occurs in the white muscles when this speed is reached. A head-to-tail effect of increasing electrical activity is noted in the red and white muscles of the grayling, the maximum electrical activity being noted in the caudal section of the body at high swimming speeds. The apparent switch from red muscle to white muscle propulsion is likely to coincide with the limit of sustainable swimming.

Neshumova (1979) studied the dynamics of the electromyographic activity (EA) of motor (red, white) and respiratory muscles, along with changes in the temperature of the red muscles of *T. arcticus baicalensis*, during swimming at a speed of 2.5 L/sec. Electrical activity and changes in the temperature of the muscles studied were higher by 30-120% in the first minutes of swimming relative to the stable values reached after further swimming at this speed. The changes were deemed to reflect the heightened activity of the motor and respiratory muscles in the first minutes of swimming. If the same holds true for European grayling, an acclimation period at a water velocity approaching 2.5 L s$^{-1}$ could be desirable.

## 2.2    European eel (*Anguilla anguilla*)

### 2.2.1  Background

The European eel (*Anguilla anguilla*) is classified as catadromous, and carries out one of the more remarkable migrations of any fish. Adult eels spawn in the Sargasso sea (Harden-Jones, 1968), and their offspring are carried eastwards by ocean currents. During the journey the larvae metamorphose first into glass eels, and then into elvers before they migrate into estuaries, and into the wholly freshwater sections of rivers. From here they search out all available habitats, and are known to travel across land on occasion. It is likely that during this searching phase that the young eels will encounter physical barriers such as weirs, and will be susceptible to entrainment into water intakes. In autumn the adult or "silver" eels migrate downstream during periods of high flow and could be drawn into water intakes. A recent decline in the numbers of eels in

many rivers has raised concerns about eel stocks and it is possible that entrainment and barriers to migration are major factors in this apparent decline.

## 2.2.2 Swimming speeds

The swimming speeds of elvers (*A. anguilla*) were examined experimentally during Phase 1 of this project, with the results being presented in the Technical Report (Clough & Turnpenny, 2000) and incorporated into the SWIMIT computer program. It was notable that, relative to body length, the younger life stages (in spring) performed better than the more developed life-stage reached by autumn of the first river year.

Other experimental studies on the swimming speeds of elvers of the European eel (McCleave, 1980) and the related American eel (*Anguilla rostrata*) (Barbin & Krueger, 1994) have been carried out. However the swimming performance of post-elver eels is less well studied.

## 2.2.3 Other aspects of swimming

A number of studies have shown a strong correlation between temperature and the migratory behaviour of eels. It has been suggested that the onset of migration is temperature-regulated for eels moving in both upstream (White & Knights, 1997) and downstream (Tesch, 1977; Vollestad *et al.*, 1986) directions.

White & Knights (1997) used mark-recapture to study the upstream migrations of elvers and juvenile eels in the Rivers Avon and Severn. Mean overall migration rate was 0.64 +/- 0.6 km day$^{-1}$, equivalent to 26.7 m hour$^{-1}$. Maximum migration rate, extrapolated from chart data, was around 2.25 km day$^{-1}$, equivalent to 93.8 m hour$^{-1}$. The speed of migration increased with temperatures above 15-16$^{o}$C. Further information on swimming speed cannot be gained as neither the proportion of time spent migrating, nor the velocity of the water they were swimming against were known. White & Knights (1997) suggested that the numbers of eels in the upper reaches of these rivers and their tributaries were influenced more by the number of man-made barriers than distance from the sea.

Sonic telemetry has been used to study the migration of eels within the marine environment. American eels (*Anguilla rostrata*) have been shown to use selective tidal stream transport in order to return to their home rivers following displacement (Barbin, 1998), making any interpretation of swimming speed very difficult. Aoyama *et al.*, (1999) stated that the mean swimming speed of Japanese silver eels (*Anguilla japonica*) in the open ocean was 0.37 m s$^{-1}$, however this is probably a net migration rate (i.e. including a passive tidal component) rather than a true swimming speed.

In freshwater, feeding eels are known to locate food using a process known as "casting". Casting is a "zigzag swimming pattern perpendicular to the mean flow that enhances the likelihood of re-entering the odor plume but does not result in significant upstream progress" (Oliver *et al.*, 1996). Any "over the ground" measures of swimming speed taken from the migration rate of feeding eels is likely to result in significant underestimates, due to the zigzag pattern described.

Eels are known to be sensitive to light, and many species of anguillid eels are considered to be nocturnally active (van Veen & Andersson, 1982) remaining concealed during the day but emerging from dusk until dawn in order to feed (Glova & Jellyman, 2000). Strong repellent reactions to light have been observed in European eels

(Hadderingh *et al*., 1999). A bright light may be a useful tool for encouraging eels to perform in swimming trials.

The swimming of eels is also known to be affected by parasites and pesticides. Oliveira & Campbell (1998) demonstrated that the parasitic trematode *Stephanostomum tenue* occurred most frequently in the pericardial cavity of elvers of American eels (*Anguilla rostrata*) where they often produced severe distension of the thoracic region and impeded swimming. The maximum swimming speed of the European eel (*A. anguilla*) is known to be reduced by infection with endoparasites including the swim bladder nematode *Anguillicola crassus* (Sprengel & Luechtenberg, 1991).

Muscular twitching, gyrating swimming movements and diminished sensory activity were cited as signs of pesticide poisoning in diazinon intoxicated eels (*A. anguilla*) (Ceron *et al*., 1997).

## 2.3    Barbel (*Barbus barbus*)

### 2.3.1    Background

Barbel (*Barbus barbus*) are highly mobile, particularly around the spawning season (Baras & Cherry, 1990; Lucas & Batley, 1996) and are classified as potamodromous. Females have been shown to be more mobile than males (Baras, 1994), and there is evidence of barbel migrating up to 318 km upstream and 301 km downstream in the River Danube (Waidbacher & Haidvogl, 1998). Barbel are known to be affected by barriers to their migration such as flow-gauging weirs, which can either impede or completely halt the upstream migration of pre-spawning fish (Lucas & Frear, 1997). Entrainment into water intakes is a possibility, particularly for early life stages. The habitat use of young barbel changes as the fish develop, and "the more the fish grow, the stronger the currents they prefer" (Freyhof, 1996). The streamlined body shape of the barbel and this natural preference for progressively stronger currents suggest that a comparatively high level of performance can be expected in swimming speed trials.

### 2.3.2    Swimming speeds

There appear to be no comprehensive measurements of the swimming speed of barbel (*Barbus barbus*) in the literature. The maximum sustained swimming speed of barbel is recorded as being 2.4 m s$^{-1}$, (Kreitmann, 1932 cited in Varley, 1967) but it is not clear how this figure was derived.

### 2.3.3    Other aspects of swimming

Lucas & Frear (1997) used radio-telemetry to study the migrations of adult barbel in the River Nidd. Measured rates of groundspeed were generally 0-0.3 m s$^{-1}$, with the fastest of 0.5 m s$^{-1}$, however swimming speed could not be calculated as the velocity of the water was not given. This study also identified that only six out of fifteen fish that attempted to pass a weir were successful, and it was suggested that the apparent inability of some individuals to ascend the weir was related to swimming performance. Water velocity on the weir was not measured in detail, but it was considered unlikely that barbel attempting to cross the weir would have to swim further than 5 m at speeds greater than 2 m s$^{-1}$.

The swimming of fish in the *Barbus* genus is known to be affected by pesticides. Sub-lethal concentrations of endosulphan caused erratic swimming in a related species *Barbus stigma* (Manoharan & Subbiah, 1982).

## 2.4 Bream (Abramis brama)

### 2.4.1 Background

Bream are potamodromous, and individuals have been shown to move up to 59 km within an Irish river system (Whelan, 1983), and more than 300 km in European rivers (Waidbacher & Haidvogl, 1998). Langford (1974) demonstrated significant movements of bream in the River Witham using sonic telemetry. Bream are known to favour the more sluggish reaches of rivers, and are likely to be particularly affected by physical barriers to their migrations. Entrainment into water intakes is a distinct possibility, particularly for young fish. Juvenile bream have been captured in water intakes on the Hampshire Avon (Solomon, 1992), and the River Meuse (Ketelaars *et al.*, 1998) suggesting that this could be a widespread problem in lowland rivers.

### 2.4.2 Swimming speeds

The swimming performance of juvenile (6-10 mm) bream (*A. brama*) from Rybinsk Reservoir (North West Russia) was studied using a small flume by Konobeeva & Volodin (1989). At current velocities of 10-12 cm $s^{-1}$, 6-64% of fish were able to resist the current for 30 min, whereas at 25-30 cm $s^{-1}$, they quickly drifted downstream against a screen. The authors noted an interesting behaviour within the shoal. By marking individuals, they showed that fish at the head of the shoal would occasionally fall to the back of the shoal to rest (presumably within the slipstream of the others), the leading position then being taken up by others. As each group of fish had been raised in separate ponds with different stocking densities it is possible that the behaviours observed were correlated to the stage of development and physiological condition of the fish. The temperatures at which the experiments were conducted are not given.

The maximum sustained swimming speed of bream is recorded as being 0.6 m $s^{-1}$ (Kreitmann, 1932 cited in Varley, 1967) but it is not clear how this figure was derived.

### 2.4.3 Other aspects of swimming

There are few references to any aspect of the swimming of bream in the literature. Langford (1974) used sonic telemetry to study the movements of bream in the River Witham and found that one individual moved over 10 km upstream in 22 hours (equivalent to a groundspeed of 454.5 m $hour^{-1}$).

# 3. SUPPLEMENTARY SPECIES OF INTEREST

## 3.1 Perch (Perca fluviatilis)

### 3.1.1 Background

The riverine migration of perch (*Perca fluviatilis*) has not been widely studied. Evidence from a fish trap on the River Thames has demonstrated that even small perch move around the river system (S. Clough, pers. obs.), and it is reasonable to class them as potamodromous. Large numbers of young of the year perch were drawn into a water intake on the River Meuse in the summer of 1996 (Ketelaars *et al.*, 1998). Barriers to migration and entrainment into water intakes could be important factors affecting perch populations in flowing waters.

### 3.1.2 Swimming speeds

There are few direct measurements of the swimming speed of perch (*Perca fluviatilis*) in the literature, and these refer to small numbers of fish. Blaxter (1969) gives the burst speeds of 100 mm and 25 mm perch as being 1.6 $ms^{-1}$ and 0.5 $ms^{-1}$ respectively (i.e. 16 $Ls^{-1}$ and 20 $Ls^{-1}$), however the time for which these speeds were maintained is not given, and these values may be closer to maximum values, as opposed to critical burst speeds. Komorov (1971) cited the maximum swimming speed of a 115 mm perch as being 1.45 $ms^{-1}$ (12.6 $ls^{-1}$); unfortunately the temperature at which the measurement was taken is not given.

### 3.1.3 Other aspects of swimming

A number of factors are known to affect the swimming behaviour and performance of perch, most notably light and temperature. Studies have shown that perch species increase their swimming activity at dusk (Helfman, 1979; Alabaster & Stott, 1978; Wang & Eckmann, 1994), but reduce or stop swimming at night (Helfman, 1979; Bergman, 1988; Wang & Eckmann, 1994; Mikheev, *et al.*, 2000). Increases in activity have also been observed at dawn (Helfman, 1979; Alabaster & Stott, 1978). This regular daily pattern of behaviour is "completely obliterated by either continuous light or continuous darkness" (Alabaster & Stott, 1978), and it appears that perch are particularly sensitive to diel changes in light intensity.

Temperature also appears to be an important factor in swimming activity and differences between seasons have been reported (Neuman, 1979; Sandstroem, 1983). Studies of perch in a lake receiving a heated effluent demonstrated that it was temperature and not season that was responsible for the difference in activity (Neuman, 1979). Research by Bergman (1987) demonstrated that routine swimming performance of perch increased with increasing temperature.

Other factors which have been shown to influence the swimming performance of perch include the acidity of the source water (Nelson, 1990), and the presence of pollutants such as tri-N-butyltin chloride (Ylae-Mononen, 1989).

## 3.2 Pike (*Esox lucius*)

### 3.2.1 Background

The majority of studies into the migration of pike (*Esox lucius*) have been carried out in lacustrine habitats, although in some of these studies the pike moved into flowing water to spawn (Clark, 1950; Franklin & Smith, 1963). Pike which are resident in rivers are also known to be mobile and can be considered potamodromous. If upstream migrations to feed or spawn are characteristic features of riverine pike behaviour, barriers to these movements could be important. Pike are generally considered to have a poor sustained swimming performance (Webb, 1994), and their association with low-velocity marginal areas may make them susceptible to entrainment into water intakes.

### 3.2.2 Swimming speeds

Academic curiosity has led to some observations of the maximum swimming speed of adult pike (e.g. Magnan, 1930; Gray, 1953), however systematic measurements of other aspects of swimming speed appear to be confined to juveniles. The swimming performance of juvenile pike (*E. lucius*) from Rybinsk Reservoir was studied experimentally by Konobeeva & Volodin (1989). These flume tests were similar in some respects to both the endurance and burst swimming trials carried out during Phase 1 of the current study. Juvenile pike of 22-34 mm in length were tested in an oval flume tank in batches of 20-25 individuals. Water flow was generated using a propeller, and velocity was increased over 1.5 hours from 7 cm s$^{-1}$ to 12 cm s$^{-1}$. The current velocity of 12 cm s$^{-1}$ (equivalent to 5.5-3.5 Ls$^{-1}$) was critical, with 74% of pike unable to maintain their position. Further tests with pike of 36-66 mm demonstrated that a current velocity of 20 cm s$^{-1}$ (equivalent to 5.5-3.0 Ls$^{-1}$) was critical with 75% unable to maintain station. The authors concluded that swimming ability improves rapidly when pike juveniles pass from the larval to the fry stage. When the data are transformed into body lengths per second, however, both groups display the same swimming speed.

Fast swimming of pike has been investigated, although interest has largely been in acceleration from a standing start during predation or escape from artificial stimuli. The pike is specially adapted to this kind of behaviour, the key features being low skin:muscle mass ratio, reducing the dead mass that has to be accelerated for each strike, and the enlarged and rearward positioned dorsal and anal fins (Videler, 1996). The fast start performance in this species is truly phenomenal and has fascinated a number of researchers (see Videler, 1996). Acceleration rates of 73-160 m s$^{-2}$ have been recorded during feeding of a 38 cm pike, and up to 245 m s$^{-2}$ in escape manoeuvres, albeit over short distances (0.21-0.43 m). In other terms the maximum of 245 m s$^{-2}$ is equivalent to an acceleration of 25$g$ ($g$ is the acceleration due to gravity of 9.8 m s$^{-2}$). By way of comparison, a space rocket launch is about 10 $g$. A maximum observed swimming speed of 7.06 m s$^{-1}$ (18.8 Ls$^{-1}$) was obtained for the same 38 cm pike (duration 1/100th of a second; temperature not stated). While these data do not provide any indication of burst speeds according to the 20s-endurance criterion required here, it is clear that any attempt measure burst speed on all but juvenile pike would be difficult. Using a tunnel having a maximum water velocity of 4 ms$^{-1}$, the maximum size of pike testable for burst speeds is likely to be around 20 cm.

### 3.3    Stone loach (Barbatula barbatula)

### 3.3.1   Background

The migratory status of the stone loach is not known.  Given their small size and cryptic nature it seems unlikely that long distance upstream migrations will be carried out on a regular basis.  However smaller local movements may well take place and could be equally important as the longer distance and more obvious migrations of larger species.  The full effect of barriers to migration or entrainment into water intakes can not be assessed until more is known about the migratory behaviour of the stone loach.

### 3.3.2   Swimming speeds

There are no references to the swimming speeds of stone loach in the literature.

### 3.3.3   Other aspects of swimming

Lucas *et al.* (1998) cite a pers. comm. from S. Axford of stone loach crossing a weir, but neither the height of the weir, nor the water velocity is given. On the other hand, Peter (1998) undertook an analysis of barriers to migration in a Swiss river system and found that stone loach, among other species, were less common above a high weir (6.5 m) than below it.  This is, however, unsurprising, as other much larger species would not be expected to pass such a high barrier, and in any case, the habitat upstream of the weir is likely to be different to that found below.

Bohmer *et al.*, (1996) demonstrated that stone loach were unable to migrate through an artificial channel without a gravel substrate.  This would suggest that stone loach use the reduced velocity of the boundary layer created by the gravel. The observation that loach are unable to migrate in the absence of gravel has obvious implications for the movements of fish over weirs and through fish passes.  Were stone loach to be chosen for future testing, conventional swimming speed protocols may need to be modified to take this into account.

There appears to be no other information in the literature concerning any aspect of the swimming of the stone loach.

### 3.4    Bullhead (*Cottus gobio*)

### 3.4.1   Background

The migratory status of the bullhead is not known. During March 2001 a single bullhead (*Cottus gobio*) was captured in a trap in a nature-like bypass channel around a weir on the River Thames (S. Clough, pers. obs.)  It is not clear whether this movement was a part of a larger scale seasonal or spawning migration, or a smaller scale daily migration associated with feeding.  It demonstrates, however, that even small cryptic benthic fishes move around their environment to some degree and may benefit from the wider access to habitat afforded by suitably designed fish passage facilities.

### 3.4.2   Swimming speeds

There appears to be no information in the literature concerning any aspect of the swimming of the bullhead.

### 3.4.3 Other aspects of swimming

Feeding generally occurs during the night and vision has an essential role in locating and capturing prey (Gaudin, 1981). This suggests that bullheads are most active after dark, and swimming speed trials may need to be conducted during reduced light conditions.

## 3.5 Lampreys (*Lampetra*, *Petromyzon* spp)

### 3.5.1 Background

There are three species of lamprey found in British freshwater waters habitats, sea lamprey *Petromyzon marinus* L., river lamprey (*Lampetra fluviatilis*) and brook lamprey (*Lampetra planeri*). As each species is similar in body form and swimming mode they will be considered together for the purposes of this review. Lampreys are known to be migratory, moving between the river and the sea (anadromous, sea lamprey) or entirely within the river (potamodromous, river lamprey, brook lamprey).

### 3.5.2 Swimming speeds

There have been comparatively few direct studies of the swimming speed of lampreys, and most have focussed on the sea lamprey *Petromyzon marinus* L.

### 3.5.3 Other aspects of swimming

The mean cruising speed during upstream migration has been recorded from telemetry studies. Stier & Kynard (1986) reported the mean ground speed of migrating lampreys to be 36 $Lmin^{-1}$, equivalent to 0.6 $Ls^{-1}$. Almeida *et al.* (2000) found that the mean ground speed of upstream migrating sea lampreys in the River Mondego was 22.5 $Lmin^{-1}$, equivalent to 0.38 $Ls^{-1}$. Extrapolating from chart data, the fastest ground speeds were in the region of 55 $Lmin^{-1}$, or 0.92 $Ls^{-1}$. Of course, measurements of ground speed do not take into account the velocity of the water in which the fish is swimming. In a tidal estuary this could correspond to either an under- or an over-estimate of the fish's swimming speed, depending on the direction of the flow. Further upstream in non-tidal section of the river estimates of ground speed will underestimate the fish's swimming speed.

## 3.6 Shads (*Alosa* spp)

### 3.6.1 Background

The Allis shad (*Alosa alosa)* and Twaite shad (*Alosa fallax*) are anadromous members of the family Clupeidae. These shoaling species move into freshwater to spawn during the spring. Although they are generally considered comparatively strong swimmers, numbers of both species in the UK have declined to very low levels, and barriers to their spawning migrations are likely to have contributed to this decline. Adults and juveniles of Twaite shad have been recorded in large numbers in the cooling water intakes of estuarine power stations (Claridge & Gardner, 1978), therefore entrainment is also a potential factor in the decline in shad populations.

### 3.6.2 Swimming speeds

There are no controlled experimental studies on the swimming of either of the European shad species in the literature. However, some aspects of the swimming of North

American members of the genus *Alosa* have been examined.  As these species are of comparable body form, swimming mode and migratory status, their swimming performance is likely to be similar in many respects to that of the European shads. Indeed, Larinier & Travade (1992) comment that observations made in France and North America have shown that their "migratory behaviour is very similar".

Shad are known to move in shoals (Larinier & Travade, 1992) and experiments to measure swimming speed should be carried out with groups of fish wherever possible. Shad also appear to be very sensitive to sudden changes in light (Larinier & Travade, 1992).  Experiments in the wild have shown that swimming activity is greater during daylight hours than during darkness, and ocean-feeding American shad (*A. sapidissima*) are known to move closer to the surface during periods of high turbidity (Dadswell *et al.,* 1983).  Tests to ascertain maximum swimming performance of shad should therefore be carried out during daylight, at uniform light intensity.

Observations made on migrating shads have provided useful information on swimming performance.  Sprint speeds of Allis shad, sustained for a period of around 6.5 seconds ranged from $3.1 - 4.7$ m s$^{-1}$, at a temperature of 16-17$^{o}$C, however the length of the fish was not given (Litaudon, 1985).  In the same study maximum speeds of 4.1-6.1 m s$^{-1}$ were recorded, but could only be maintained for "a few seconds".  In a similar study with American shad, Weaver (1965) measured the distance swum by more than 8,000 fish in a 30 m channel with water velocities of between 3.5 and 4.15 m s$^{-1}$ at a water temperature of 21$^{o}$C. Weaver estimated the maximum swimming speed of the majority of shad to be between 4.3 and 4.6 ms$^{-1}$, however individual lengths were not given.

### 3.6.3   Other aspects of swimming

A number of factors affect the swimming performance of shads and performance in swimming speed trials can be expected to be high in comparison with the species tested to date.  American shad (*Alosa sappidissima*) made to swim in a respirometer at velocities of  between 1.0 and 2.3 bl s$^{-1}$ demonstrated metabolic rates that were intermediate between salmonids and fast-swimming perciforms, including tunas (Leonard *et al*., 1999).  From other work, Leonard & McCormick (1999) concluded that changes in haematological physiology occurring during upstream migration may increase swimming performance and migratory success in American shad.

Conversely, Larinier & Travade (1992) stated that "the shad is a poorer swimmer than the salmon or sea trout," "velocities of around 3.5 - 4 m s$^{-1}$ over a distance of a few metres constitute an obstacle" and "that velocities of around 2 m s$^{-1}$ constitute a major difficulty for some of them when the distance to be passed is more than several tens of metres."

Studies on the swimming behaviour of European shads are comparatively rare. Steinbach *et al*., (1986) demonstrated that water temperature had a pronounced effect on the swimming speed of radio-tagged Allis shad (*Alosa alosa*) in the River Loire, and that migrations were inhibited at times when temperatures fell below 12 degrees C.  At other times upstream migration occurred at an average rate of 20 km day$^{-1}$ (*c.* 0.23 ms$^{-1}$).  Bellariva & Belaud (1998) attributed the earlier arrival of Allis shad at a fish lift to the disappearance of an old weir which had previously impeded migrations.

Haro *et al*., (1999) investigated the passage and transit time of adult upstream-migrant American shad (*A. sapidissima*) in standard Denil and Alaska steeppass fishways under semi-controlled conditions. Percent of American shad passed per unit time (percent passage) increased with temperature, while time required to ascend from the fishway entrance to the exit (transit time) decreased with increasing temperature, suggesting improved swimming performance at higher temperatures. Increasing fishway slope decreased percent passage of American shad in both types of fishway, however transit time decreased with increasing slope, and through-water swimming speed was increased under these conditions. This suggests that American shad regulate their swimming speed through Denil-type fishways below maximal values, and that turbulence and air entrainment may influence percent passage more than longitudinal water velocity (Haro *et al*., 1999).

This suggestion is in agreement with the findings of Larinier & Travade (1992), who state that shad prefer regular water currents with parallel flows and "seem to avoid very turbulent zones and emulsified water" and that they move with "far more difficulty than salmonids" in such areas. Other observations include "shad do not leap, but generally pass obstructions by swimming" and "The shad is a surface fish: it must therefore be provided with fish passage facilities at the surface" (Larinier & Travade, 1992).

The ocean migration rates of American shad (*A. sapidissima*), estimated from tag returns, averaged 21 km day$^{-1}$ (approximately equivalent to 0.24 m s$^{-1}$) and appears to be regulated by temperature (Leggett, 1977). However the speed at which the fish were swimming can not be calculated, as the route taken by the fish it is not known.

# 4. DISCUSSION

Robust data regarding the maximum, burst and sustained swimming speeds of the test species are virtually absent from the literature. Data for the additional species of interest are also sparse or absent. Definitions of burst, maximum, cruising and sprint speeds vary between authors and are not always given. In addition, the full experimental conditions and handling regimes are rarely reported, and essential details such as fish length or water temperature are often omitted. There are some interesting references to measured rates of ground speed, however these are only indicative of net migration rates and cannot be construed as indicators of swimming ability.

The following paragraphs summarise the key points for the species of interest.

## 4.1 Grayling

Comments regarding swimming ability are contradictory and indicate that poor performance could be experienced in laboratory trials. Grayling are notoriously poor at passing obstacles and may have a comparatively low burst swimming capacity. Observations of the natural behaviour and habitat use of grayling in rivers have shown that areas with high water velocities are favoured, and performance in endurance swimming trials could be relatively good. The observation that electrical activity and temperature of the muscles of grayling stabilise after a few minutes of swimming suggests that an acclimation period at a water velocity approaching $2.5 \ L \ s^{-1}$ might be beneficial, although this assumes that fish in the wild are similarly active.

## 4.2 Barbel

Barbel are known to migrate extensively within rivers, crossing weirs in the process. The behaviour and habitat use of barbel in the wild suggest a high level of performance can be expected in swimming trials.

## 4.3 Bream

The apparent preference for the slower reaches of rivers may be expected to correspond with a comparatively low swimming ability. Tracking studies have shown that bream are highly mobile within rivers, and barriers to their migrations affect their distribution. Juvenile bream are known to be drawn into water intakes and entrainment of young life stages could be particularly important for this species.

## 4.4 Eel

Given the comparatively poor performance of elvers of the European eel tested during Phase 1 of the current study, very high velocities are unlikely to be required for even the largest size category of eels. Standard test protocols should be suitable for burst and endurance swimming, however the smallest size group will require modifications to the mesh size of the standard flumes, and appropriate recalibration to take account of fish using boundary layers. Eels are sensitive to light, and bright lights could be useful tools to influence behaviour in swimming trials.

## 4.5    Species for future testing

Shad and perch appear to be particularly sensitive to factors such as light and water temperature.  These factors would need to be taken into account if these species are selected for future testing.  Motivation to swim to their maximum ability may be a problem for cryptic benthic species such as stone loach and bullhead.  These fishes may need an innovative approach based on successful passage of a known velocity, rather than the standard burst and endurance tests.

# 5. REFERENCES

Alabaster, J. S. & Stott, B. (1978). Swimming activity of perch, *Perca fluviatilis* L. Journal of Fish Biology 12, 6, 587-591.

Almeida, P. R., Silva, H. T. & Quintella, B. (2000). The migratory behaviour of the sea lamprey *Petromyzon marinus* L., observed by acoustic telemetry in the River Mondego (Portugal). Advances in Fish Telemetry. A. Moore & I. Russel eds 264pp.

Aoyama, J., Hissmann, K., Yoshinaga, T., Sasai, S., Uto, T. & Ueda, H. (1999). (Abstract only). Swimming depth of migrating silver eels Anguilla japonica released at seamounts of the West Mariana Ridge, their estimated spawning sites. Marine ecology progress series. Oldendorf [Mar. Ecol. Prog. Ser.], 186, pp. 265-269.

Baras, E. (1994). Constraints imposed by high population densities on behavioural spawning strategies in the barbel, *Barbus barbus*. *Folia zoologica Brno* **43**, 255-266.

Baras, E. & Cherry, B. (1990). Seasonal activities of female barbel *Barbus barbus* (L.) in the River Ourthe (Southern Belgium) as revealed by radio-tracking. Aquatic Living Resources 7, 181-189.

Barbin, G. P. (1998) The role of olfaction in homing and estuarine migratory behavior of yellow-phase American eels. Canadian Journal of Fisheries and Aquatic Sciences 55, 3, 564-575.

Barbin, G. P. & Krueger, W. H. (1994). Behaviour and swimming performance of elvers of the American eel, *Anguilla rostrata*, in an experimental flume. Journal of Fish Biology 45, 117-121.

Bellariva, J-L. & Belaud, A. (1998). Environmental factors influencing the passage of Allice shad Alosa alosa at the Golfech Fish Lift on the Garonne River, France. In: M. Jungwirth, S. Schmutz & S. Weiss (eds.). Fish Migration and Fish Bypasses. Fishing News Books. pp 171-179.

Bergman, E. (1987). Temperature-dependent differences in foraging ability of two percids, *Perca fluviatilis* and *Gymnocephalus cernuus*. Environmental Biology of Fishes 19, 1, 45-53.

Bergman, E. (1988). Foraging abilities and niche breadths of two percids, *Perca fluviatilis* and *Gymnocephalus cernua*, under different environmental conditions. Journal of Animal Ecology 57, 2, 443-453.

Blaxter, J. H. S. (1969). Swimming speeds in fish, FAO fisheries report No. 62 Vol 2.

Bohmer, J., Kappus, B., Jansen, W., Nill, A., Beiter, T. & Rahmann, H. (1996). Conditions for successful upstream passage through fishways as derived from field data and an experimental flume. International Conference on Fish Migration and Fish By-pass Channels. Vienna 1996.

Ceron, J.J., Sancho, E., Ferrando, M. D., Gutierrez, C. & Andreu, E. (1997). Changes in carbohydrate metabolism in the eel *Anguilla anguilla*, during short-term exposure to diazinon. Toxicological and Environmental Chemistry 60, no. 1-4, pp. 201-210.

Claridge, P. N. & Gardner, D. C. (1978) Growth and movements of the Twaite shad *Alosa fallax* (Lacepede) in the Severn Estuary. Journal of Fish Biology, 12, 203-211.

Clark, C. F. (1950). Observations on the spawning habits of the northern pike, *Esox lucius*, in north-western Ohio. Copeia 4 285-288.

Clough, S. C. & Turnpenny, A. W. H. (2000). Swimming Speeds in Fish – Phase 1. Environment Agency National R&D Technical Report W251.

Dadswell, M. J., Melvin, G. D. & Williams, P. J. (1983). Effect of turbidity on the temporal and spatial utilization of the inner Bay of Fundy by American shad (*Alosa sapidissima*) (Pisces: Clupeidae) and its relationship to local fisheries. Canadian Journal of Fisheries and Aquatic Sciences 40, suppl.1, 322-330.

Domenici, P., Steffensen, J. F. & Batty, R. S. (2000). The effect of progressive hypoxia on swimming activity and schooling in Atlantic herring. Journal of Fish Biology 57, 1526-1538.

Eckmann, R. & Imbrock, F. (1996). Distribution and diel vertical migration of Eurasian perch (*Perca fluviatilis* L.) during winter. Annales Zoologici Fennici 33, 3-4, 679-686.

Franklin, D. R. & Smith, L. L. Jr. (1963). Early life history of the northern pike, *Esox lucius* L., with special reference to the factors influencing numerical strength of year classes.

Freyhof, J. (1996). Distribution of YOY-barbel *Barbus barbus* (L.) in the River Sieg/Germany. Conservation of endangered freshwater fish in Europe. Birkhaeuser verlag, basel (Switzerland) pp. 259-267.

Gaudin, P. (1981). (Abstract only) Eco-ethology of a benthic fish, Cottus gobio L. (Cottidae): Distribution, feeding and relationships with trout, Salmo trutta Trutta L. Uer sciences de la nature, dep. Biol. Anim. Ecol., Villeurbanne (France) , 1981, 185 pp.

Glova, G. J. & Jellyman, D. J. (2000) Size-related differences in diel activity of two species of juvenile eel (*Anguilla*) in a laboratory stream. Ecology of Freshwater Fish 9, no. 4, pp. 210-218.

Gray, J. R. (1953). The locomotion of fishes. Essays Mar. Biol. Cited in Beamish (1978).

Harden-Jones, F. R. (1968). Fish Migration. Arnold, London.

Haro, A., Odeh, M., Castro-Santos, T. & Noreika, J. (1999). Effect of slope and headpond on passage of American shad and blueback herring through simple Denil and deepened Alaska steeppass fishways. North American Journal of Fisheries Management 19, 1, 51-58.

Helfman, G. S. (1979). Twilight activities of yellow perch, *Perca flavescens*. Journal of the Fisheries Research Board of Canada 36, 2, 173-179.

Hughes, N. F. & Kelly, L. H. (1996). A hydrodynamic model for estimating the energetic cost of swimming maneuvers from a description of their geometry and dynamics. Canadian Journal of Fisheries and Aquatic Sciences 53, 11, 2484-2493.

Jungwirth, M. (1996). Bypass channels at weirs as appropriate aids for fish migration in rhithral rivers. Regulated Rivers: Research & Management 12, 4-5, 483-492.

Ketelaars, H. A. M., M. Klinge, A. J. Wagenvoort, J. Kampen and S. (A.) M. A. Vernooij. 1998. Estimate of the amount of 0+ fish pumped into a storage reservoir and indications of the ecological consequences. Internat. Rev. Hydrobiol. 83: 549-558.

Komarov, V. T. (1971). Speeds of fish movement. Zoological Herald 4, 67-71.

Konobeeva, V. K. & Volodin, V. M. (1989. Experimental studies on the swimming ability of pike (*Esox lucius*), bream (*Abramis brama*) and roach (*Rutilus*

*rutilus*) juveniles from Rybinsk Reservoir.  Journal of Ichthyology 29, 5, 83-93.

Langford, T. E. (1974).   Trials with ultrasonic tags for the study of coarse fish behaviour and movements around power station outfalls.  Journal of the Institute of Fisheries Management 5, 3, 61-62.

Larinier, M. & Travade, F. (1992).  Designing fish passage facilities for shad.  French Journal of Fishing and Fish Breeding 326-327. pp 117-122.

Leggett, W. C. (1977).  Ocean migration rates of American shad (*Alosa sapidissima*).  J. Fish. Res. Board Can., 34(9), 1422-1426.

Leonard, J. B., & McCormick, S. D. (1999).  Changes in haematology during upstream migration in American shad.  Journal of Fish Biology 54, 6, 1218-1230.

Leonard, J. B., Norieka, J. F., Kynard, B., &  McCormick, S. D. (1999).  Metabolic rates in an anadromous clupeid, the American shad (*Alosa sapidissima*).  Journal of Comparative Physiology 169, 4/5, 287-295.

Litaudon, A. (1985).  Preliminary observations on shad (Alosa alosa) passing the Saint-Laurent-des-Eaux (Loire) sill.  EDF report HE/31/85-37. 63pp. *Cited in* Larinier & Travade (1992).

Lucas, M. C. & Batley, E. (1996).  Seasonal movements and behaviour of adult barbel *Barbus barbus*, a riverine cyprinid fish: implications for river management.  Journal of Applied Ecology 33, 1345-1358.

Lucas, M. C. & Frear, P. A. (1997).  Effects of a flow-gauging weir on the migratory behaviour of adult barbel, a riverine cyprinid.  Journal of Fish Biology 50, 382-396.

Lucas, M. C., Thom, T. J., Duncan, A. & Slavik, O. (1998).  Coarse Fish Migration – Occurrence, Causes and Implications.  Environment Agency National R&D Technical Report W152. 161pp.

Magnan, A. (1930).  Les characteristiques geometriques et physiques des poissons.  Annales des sciences naturelles 13: 1971-81 *cited in* Blake (1983).

Manoharan, T. & Subbiah, G.N. (1982).  Toxic and sublethal effect of endosulfan on Barbus stigma (Pisces: Cyprinidae). PROC. INDIAN ACAD. SCI., ANIM. SCI., vol. 91, no. 6, pp. 523-532.

Matyukhin, V. A., Alikin, Yu.S., Stolbov, A.ya. & Turetskij, V. I.  (1973).  An experimental study of fish swimming efficiency. Bionika,  7,  31-37.

Matyukhin, V. A. & D'yachenko (1976).  Electrical activity of the red and white muscles of the Baikal grayling, *Thymallus arcticus baicalensis*, at different swimming speeds.  Journal of Ichthyology 16, 1, 130-135.

McCleave, J. D. (1980).  Swimming performance of European eel (*Anguilla anguilla* L.) elvers.  Journal of Fish Biology 16, 445-452.

Mikheev, V. N., Mikheev, A. V., Pasternak, A. F. & Valtonen, E. T.  (2000).  Light-mediated host searching strategies in a fish ectoparasite, *Argulus foliaceus* L. (Crustacea: Branchiura) Parasitology, 120,  4,  409-416.

Nelson, J. A. (1990).  Muscle metabolite response to exercise and recovery in yellow perch (*Perca flavescens*): Comparison of populations from naturally acidic and neutral waters. Physiological Zoology 63, 5, 886-908.

Neshumova,T. V. (1979).  The dynamics of changes in the electrical activity and temperature of different types of muscles in the Lake Baikal grayling, *Thymallus arcticus baicalensis*, during prolonged  swimming.  Journal of Ichthyology 19, 1, 139-143.

Neuman, E. (1979). Activity of perch, *Perca fluviatilis* L. and roach, *Rutilus rutilus* (L.), in a Baltic bay, with special reference to temperature. Rep. Inst. Freshwater Res., Drottningholm 58, 107-125.

Northcote, T. G. (1995). Comparative biology and management of Arctic and European grayling (*Salmonidae, Thymallus*). Reviews in Fish Biology and Fisheries 5, 141-194.

Northcote, T. G. (1998). Migratory behaviour of fish and its significance to movement through riverine fish passage facilities. In: M. Jungwirth, S. Schmutz & S. Weiss (eds.). Fish Migration and Fish Bypasses. Fishing News Books. pp 3-18.

Oliveira, K. & Campbell, R. (1998). The occurence and pathological effects of *Stephanostomum tenue* (Digenea: Acanthocolpidae) metacercariae in elvers of the American Eel. Journal of Fish Biology 53, no. 3, pp. 690-692.

Oliver, S. J., Grasso, F. W. & Atema, J. (1996). Filament tracking and casting in American elvers (*Anguilla rostrata*). Biological Bulletin, Marine Biological Laboratory, Woods Hole, vol. 191, no. 2, pp. 314-315.

Persat, H. (1996). Threatened populations and conservation of the European grayling, *Thymallus thymallus* (L. 1758). In: Conservation of Endangered Freshwater Fish in Europe (eds A. Kirchhofer & D. Hefti) Birkhauser Verlag, Basel, Boston, Berlin. pp 233-247.

Pedersen, J. (2001). Hydroacoustic measurement of swimming speed of North Sea saithe in the field. Journal of Fish Biology 58, 1073-1085.

Peter (1998).

Sagnes, P., Champagne, J. & Morel, R. (2000). Shifts in drag and swimming potential during grayling ontogenesis: relations with habitat use. Journal of Fish Biology 57, 1, 52-68.

Sandstroem, O. (1983). Seasonal variations in the swimming performance of perch (*Perca fluviatilis* L.) measured with the rotatory-flow technique. Canadian Journal of Zoology 61, 7, 1475-1480.

Solomon, D. J. (1992). Diversion and entrapment of fish at water intakes and outfalls. National Rivers Authority Research and Development Report 1.

Sprengel, G., Luechtenberg, H. (1991). Infection by endoparasites reduces maximum swimming speed of European smelt *Osmerus eperlanus* and European eel *Anguilla anguilla*. Diseases of Aquatic Organisms 11, 31-5.

Steinbach, P., Gueneau, P., Autuoro, A. & Broussard, D. (1986). Radio-tracking of Atlantic shads in the river Loire. Bulletin Francais de la Peche et de la Pisciculture. 302, 106-117.

Stier, K. & Kynard, B. (1986). Movements of sea-run sea lampreys, *Petromyzon marinus*, during the spawning migration in the Connecticut river. Fishery Bulletin, 84, 749-753.

Stolvov, A.Ya. & Alikin,Yu.S. (1977). Temperature dependence of active metabolism and swimming speed of the Baikal grayling, *Thymallus arcticus baicalensis* Journal of Ichthyology 17, 1, 178-179.

Svendsen, J. C., Skov, J., Bildsoe, M. & Steffensen, J. F. (2003). Intra-school positional preference and reduced tail beat frequency in trailing positions in svhooling roach under experimental conditions. Journal of Fish Biology 62, 834-846.

Tesch, F.-W. (1977). The Eel: Biology and management of anguillid eels. Chapman & Hall, London.

van Veen, T. & Andersson, M. (1982). Threshold for synchronization of locomotor activity to visible radiation in the eel *Anguilla anguilla*. Oikos, 38, no. 1, pp. 21-26.

Varley, M. E. (1967). British Freshwater Fishes. Fishing News (Books) Ltd. London. 148pp.

Videler, J. J. (1996). Fish Swimming. London, Chapman & Hall, 260 pp.

Vollestad, L. A., Jonsson, B., Hvidsten, N. A., Naesje, T. F., Haraldstad, O. & Ruud-Hansen, J. (1986). Environmental factors regulating the seaward migration of European silver eels (*Anguilla anguilla*). Canadian Journal of Fisheries & Aquatic Science 43, 1909-1919.

Wagner, G. N., McKinley, R. S., Bjorn, P. A. & Finstad, B. (2003). Physiological impact of sea lice on swimming performance of Atlantic salmon. Journal of Fish Biology 62, 1000-1009.

Wang, N. & Eckmann, R. (1994). Distribution of perch (*Perca fluviatilis* L.) during their first year of life in Lake Constance. Hydrobiologia 277, 3, 135-143.

Waidbacher, H. & Haidvogl, G. (1998). Fish migration and fish passage facilities in the Danube: past & present. In: M. Jungwirth, S. Schmutz & S. Weiss (eds.). Fish Migration and Fish Bypasses. Fishing News Books. pp 85-98.

Weaver, C. R. (1965). Observations on the swimming ability of adult American shad (*Alosa sapidissima*). Trans. Am. Fish. Soc., 94, 4, 382-385. *cited in* Larinier & Travade (1992).

Webb, P. W. (1994). The biology of fish swimming. In: L. Maddock, Q. Bone & J. M. V. Rayner (eds.). Mechanics and Physiology of Animal Swimming. Cambridge University Press. pp 45-62.

Whelan, K. F. (1983). Migratory patterns of bream *Abramis brama* L. shoals in the River Suck system. Irish Fisheries Investigation Series A 23 11-15.

White, E. M. & Knights, B. (1997). Dynamics of upstream migration of the European eel, *Anguilla anguilla* (L.), in the Rivers Severn and Avon, England, with special reference to the effects of man-made barriers. Fisheries Management and Ecology 4, 311-324.

Ylae-Mononen, L. (1989). The effects of tri-N-butyltin chloride (TBTC) on the early life stages of perch (*Perca fluviatilis* L.) in brackish water. Aqua Fennica 19, 2, 129-133.

Ytrestoyl, T., Finstad, B. & McKinley, R. S. (2001). Swimming performance and blood chemistry in Atlantic salmon spawners exposed to acid river water with elevated aluminium concentrations. Journal of Fish Biology 58, 1025-1038.