Swimming Speeds in Fish: phase 2

ENVIRONMENT
AGENCY

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- **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

ACKNOWLEDGEMENTS

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Glossary

Burst swimming speed:

The highest swimming speed that can be maintained by a fish for ≥ 20 seconds.

Maximum swimming speed:

The theoretical maximum swimming speed that a fish is capable of achieving. Maximum speed can be determined through muscle twitch experiments.

Prolonged swimming speed:

The highest swimming speed which can be maintained for between 20 seconds and 200 minutes.

Sustained swimming speed:

The maximum swimming speed which can be maintained for in excess of 200 minutes.

Critical burst swimming speed:

Is an approximation of the final velocity attained before exhaustion, in tests where the speed is increased by incremental amounts at fixed time intervals.

Exhaustion:

The point at which a fish in a swimming speed trial can no longer maintain its position against the flow and is subsequently carried downstream and caught against the screen. Exhaustion in this context therefore contains a behavioural component, and may not necessarily correspond to physiological exhaustion.

Fish length:

Fish lengths were recorded as fork lengths for barbel, bream and grayling, and as standard length for eels.

Stride length:

The distance that the fish moves forward for one complete tailbeat cycle.

Notation

s.l. = Standard length

bl s^{-1} = body lengths per second

EXECUTIVE SUMMARY

Background/Need

Many fish species are known to migrate extensively around river systems on both daily and seasonal timescales, these migrations serving important functions in the life histories of the fish. Man has caused various detrimental impacts on riverine environments, not least by the construction of impassable barriers in the form of weirs, dams and other river management structures. The entrainment of migrating and resident fish into potable and industrial water intakes is also of concern. The financial investment in fish passes to facilitate fish migrations is considerable, as is the cost of screens to prevent entrainment.

Effective design of these structures requires robust data on the swimming performance of river fishes under a wide range of conditions. Although some information on fish swimming performance is to be found in the scientific literature, the data are often based on inadequate numbers of fish tested at a single or unstated water temperature, and a more thorough study was warranted.

Main objectives/Aims

Phase 1 of the current project collected robust swimming performance data and developed a computer model ('SWIMIT') to describe the swimming performance of five British freshwater fish species. The objectives of Phase 2 of the project were to gather comparable data for further species and lifestages, and to update the 'SWIMIT' computer model to cover all the species and lifestages tested to date.

Phase 2 study species were:

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

In parallel to this work, a study of the swimming speeds of smelt (*Osmerus eperlanus*) was being conducted on behalf of Thames Water Utilities Ltd (TWU). TWU agreed that the results of the smelt study could be included in the SWIMIT v.2.0 programme, and the output from the smelt work could be appended to this report.

A literature review revealed few robust swimming performance data for the species of interest (Clough & Turnpenny, 2003). Swimming speed experiments were designed to discover the limits of both burst and sustained endurance swimming, and were compatible with those used in Phase 1 of the study. Larger numbers of fish were tested in Phase 2 compared with Phase 1 which should increase the confidence in the results. To ensure a broad coverage, fish of different sizes were tested at a representative range of temperatures. Eels and the larger size classes of grayling were collected from the wild and the bream, barbel and smallest grayling were of hatchery origin. All fish were held in outdoor stock tanks prior to testing, and were exercised using internal re-circulating pond pumps. The swimming tests were conducted in the same purpose-built apparatus as was used during Phase 1, repeating standard methodologies. A large (8 m long) flume tank was used to examine the endurance swimming of fish over a 200 minute period. This flume was modified prior to Phase 2 by replacing the paddle wheel drive system (used in

Phase 1) with a propeller, allowing higher speeds to be achieved. Burst swimming performance was tested in a high-speed tunnel, where a large pump generated flow. In burst swimming tests, speed through the tunnel was increased incrementally until the fish could no longer maintain their position. From this, the Critical Burst Swimming Speed (CBSS) was estimated.

Results

Swimming speed trials covered three size classes of barbel, eels and grayling, and one size class of bream. For barbel, bream and grayling burst and endurance tests were conducted within three temperature categories, covering the likely range experienced by migrating fishes in the wild. Eels were only tested in the two highest temperature categories, as they are generally considered to be inactive at low temperatures. In total, over 11,000 fish swimming performance tests were conducted, with in excess of 9,000 endurance observations and more than 1,400 in burst tests.

Endurance swimming ability generally showed an increase with increasing fish length, a trend which was particularly noticeable in barbel and grayling (Figure ES1). The effect of increasing temperature was less consistent, and varied among species. Although barbel and bream showed the expected increase in sustained swimming performance with increasing temperature, both the small and large grayling performed less well at the $>15^{o}C$ temperature category compared with the $10\text{-}15^{o}C$ category (Figure ES1). Grayling are generally considered to be a coldwater species, and it is likely that the data reflect a real reduction in their swimming capacity, or at least their motivation to sustain high speeds for long periods, although the possibility that some of the large grayling were not in perfect health is also acknowledged.

In general, the mean CBSS tended to increase with increasing fish length (Figure ES2). There are however anomalies with regard to the effect of temperature, notably the tendency for reduced performance at high temperatures seen in both bream and the larger size classes of grayling. With the wild grayling, again some may not have been in perfect health, however this would not explain the reduced warm-temperature performance of the hatchery reared grayling, or of the bream. It is not clear why the burst swimming performance of these species falls with increasing temperature, but it could reflect a reduction in their motivation to achieve maximum performance, rather than a reduced physiological ability at higher temperatures.
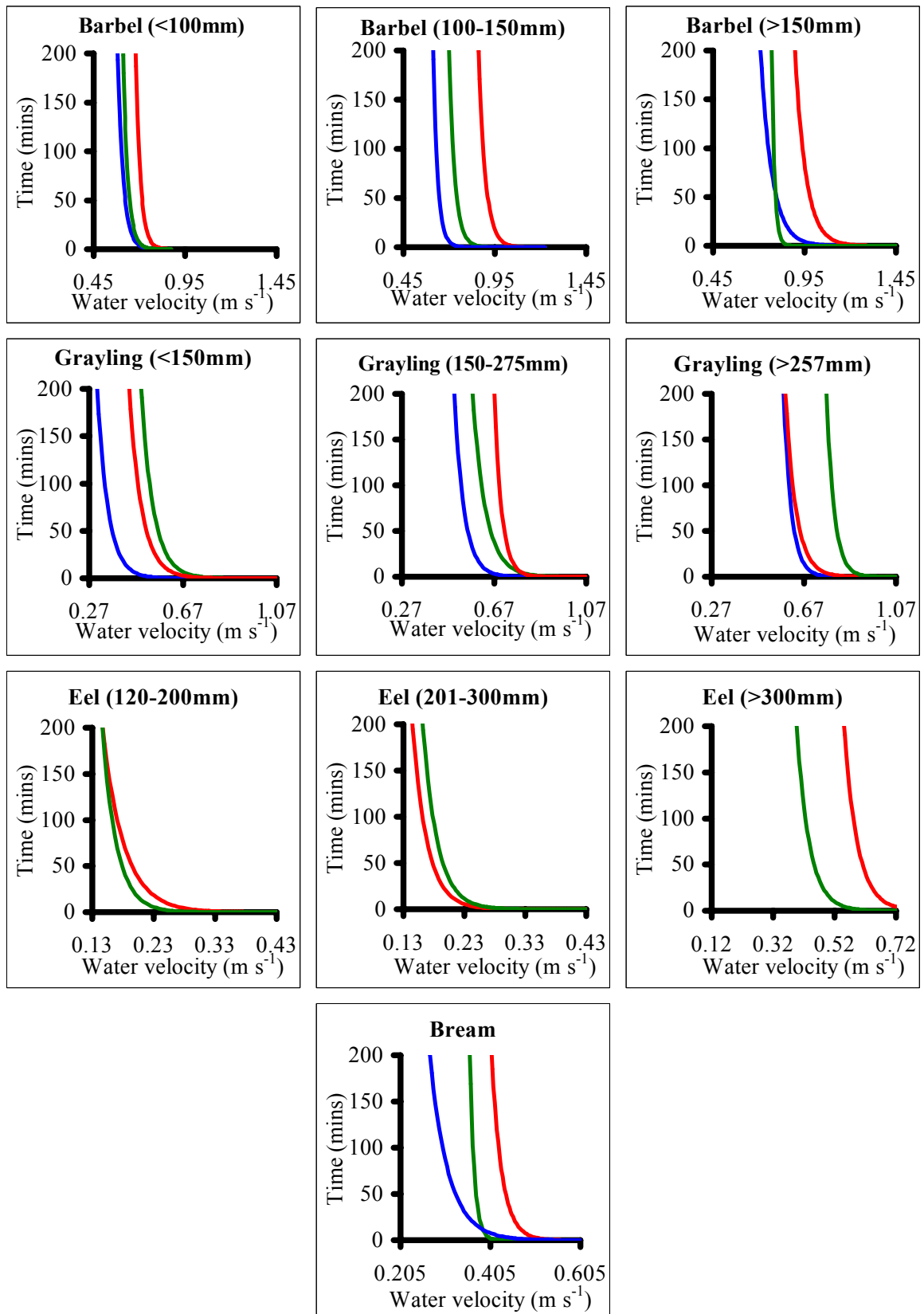
Figure ES1. Exponential plots showing median endurance time against fish length. Blue line <10°C; green line 10-15°C; red line >15°C.
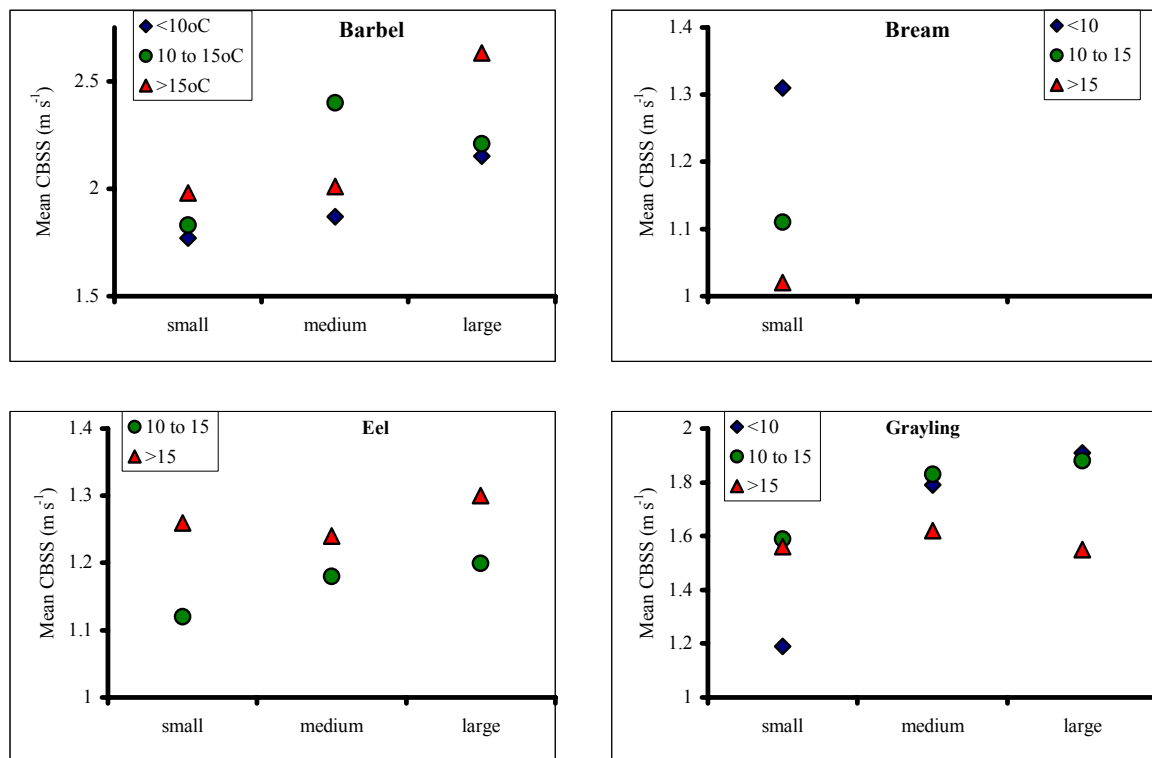
Figure ES2. Mean CBSS graphs for each species and size class tested.

Conclusions & Recommendations

1. Large numbers of fish were tested in both burst and endurance trials, and robust data sets were generated.

2. There was a high degree of individual variation in fish performance both within and between tests.

3. Barbel consistently exhibited superior swimming performance to any of the other species tested in Phase 2.

4. Wild grayling were particularly difficult to keep in captivity, especially during the summer. The same problem was not encountered with hatchery-reared individuals.

5. The swimming performance of grayling shows a general decline at high water temperatures, in both burst and endurance tests.

6. Eels are generally poor swimmers and performed less well in swimming trials than the other species tested to date.

7. It appears that for small bream, at the coldest temperatures, the start velocity can influence performance in burst swimming trials, but this does not appear to be the case at the highest temperatures.

8. The performance of bream in endurance swimming trials shows a general increase with increasing water temperature. This is in direct contrast to the significant reduction in CBSS with increasing temperature.

9. The computer program SWIMIT v.2.0 may be used to estimate swimming speeds of the average or median fish of a given size at a given water temperature, and also the

90%ile value. The latter helps to take account of the spread of performance within the population.

10. The experimental data generated here under laboratory conditions may include some fish that performed less well than they would in the wild, for reasons of handling and confinement. Also, they were tested in smooth channels with minimal boundary layer, unlike in many field situations where gravel or rocky substrates occur. The data therefore probably underestimate true performance in natural channels, thereby giving a margin of safety.

11. Provided that the hydraulics of the structure are properly taken into account, the data provided here, accessible via the SWIMIT v.2.0 computer program, provide a good way of factoring fish swimming performance into design of engineered structures such as water intakes and fish passes.

12. Literature data regarding the swimming ability of other native riverine species including pike, perch and larger bream are sparse and further testing with these species would be justified.

13. Minor riverine species such as ruffe, bullhead, bleak and stone loach have generally not been considered in studies of swimming performance, and may warrant further investigation.

KEY WORDS

Swimming, speed, fish passes, water intakes, weirs, barbel (*Barbus barbus*), Grayling (*Thymallus thymallus*), eel (*Anguilla anguilla*), bream (*Abramis brama*), smelt (*Osmerus eperlanus*).

1. INTRODUCTION

1.1 Background

A detailed background to the importance of understanding the limits of fish swimming ability was given in Phase 1 of this project (Clough & Turnpenny, 2000). To avoid excessive repetition, the salient points are summarised below:

During normal day-to-day life most river fishes use only a small proportion of their available swimming capacity, with excess capacity being used, for example, to escape from predators, migrate past obstructions and to avoid being displaced during floods. There is growing scientific evidence that many non-salmonid riverine fishes migrate extensively for feeding, refuging and recolonisation following displacement. The activities of man have impacted on riverine fish populations in many ways, not least through the construction of weirs, dams, and locks. Fish passes aimed at reducing the impact of physical barriers on fish migrations have generally been designed to facilitate the passage of strongly swimming migratory salmonids, not coarse fish. Also, there is the risk of migrating and resident fish being drawn ('entrained') into industrial and potable water intakes or hydroelectric turbines. To avoid entrainment, or impingement on physical screens, the fish must be able to swim faster than the intake velocity. The development of appropriate swimming performance data for common riverine species is therefore required to provide design criteria for future fish pass and intake construction and for other enhancement, protection and ameliorative measures.

1.2 Terms of Reference

A number of variables influence the swimming performance within a given species, most notably fish size and water temperature. There is also a degree of inter-individual variation resulting from differences in genetic make-up, health and condition. With this in mind the aims of the project were to:

1. Carry out a review of available fish swimming literature.

2. Measure for different size classes of barbel, bream, grayling and eels, at three water temperatures representative of the seasonal range:

    i. endurance swimming performance at a range of speeds;

    ii. burst swimming ability.

3. Extend the 'SWIMIT' v.1.0 computer programme to accommodate the species and life-stages tested, covering a representative range of fish sizes and water temperatures.

2. THEORETICAL BACKGROUND

A review of existing scientific literature on fish swimming speed was carried out at the start of Phase 1 of this project, and updated during Phase 2 (Clough & Turnpenny, 2003). Literature data relating to the project species of interest were limited, and those that were presented varied in experimental methodology. A detailed theoretical background to different aspects of fish swimming was given in Phase 1 of this study (Clough & Turnpenny, 2000). Some aspects, such as the effects of wave drag, and swimming whilst partially submerged, are not relevant to Phase 2 of the project, and have been omitted. A summary of the most relevant material is given below.

The majority of fish species use two main types of muscle for swimming. Red muscle contracts only when oxygen is available to the cells. Any restriction in oxygen availability limits its rate of performance (Wardle, 1977). In the wild, fish use red muscle to maintain position in the flow, and for daily movements and seasonal migrations within a river system. Red muscle is also likely to be employed by fish in the ascent of low velocity baffled fish passes, and to resist entrainment at water intakes. Endurance swimming trials were designed to test the limits of red muscle driven swimming performance.

White muscle can contract in the absence of oxygen, and becomes exhausted when all the glycogen stored in its cells has been converted to lactic acid. Replacing the glycogen requires oxygen, and can take up to 24 hours (Wardle, 1977). At burst swimming speeds, energy is almost totally supplied by the white muscle (Wardle, 1980). White muscle is used during escape from predators or when catching fast-moving prey, and will be used to ascend pool-and-traverse type fish passes, and during leaping. White muscle will also be used in the ascent of baffled fish passes and weir slopes when the velocity exceeds the capacity of red muscle. Burst swimming trials were designed to test the limits of white muscle swimming performance.

A third 'intermediate' muscle type, known as pink muscle, is found in some species, including cyprinids. Pink muscle fibres are recruited into the swimming process after the red fibres and before the white fibres become active.

3.   METHODS

3.1   Swimming Speed Experiments

Experiments were carried out with barbel (*Barbus barbus*), bream (*Abramis brama*), grayling (*Thymallus thymallus*) and eels (*Anguilla anguilla*). A wide range of fish lengths and temperatures was investigated. Test fish were divided into three categories according to length, except bream, which were only tested within one size category (Table 3.1). Fish from each of these categories were tested within three different temperature ranges, 5-10°C, 10-15°C and >15°C. Eels are generally inactive during the winter, and were not tested within the lowest temperature band. Some fish were tested more than once, with a minimum recovery period of 48 hours between tests. In the results, the total number of fish tested is denoted by n_2, whereas n_1 gives the number of different individuals tested.

Table 3.1. Size categories used for swimming speed tests.

Species	Small size category (mm)	Medium size category (mm)	Large size category (mm)
Barbel	<100	100-150	>150
Grayling	<150	150-275	>275
Eel	120-200	201-300	>300
Bream	One size (<100mm)		

3.2.   Fish supplies

Test fish were retained in 2 m-square stock tanks at Fawley Aquatic Research Laboratories, having been collected from flowing water environments where possible. Fish were collected as required, usually by electrofishing, and held for at least one week prior to testing. Where wild, riverine sources of the required species and size classes were unavailable, hatchery reared or stillwater stocks were used, but only as a last resort. A full list of fish used in the swimming speed trials, including source, number and date collected is given in the appendix (Table A1.).

3.2.1. Barbel

The stocks of barbel were obtained mostly at the beginning of the project from Hampshire Carp Hatcheries and Calverton fish farm. Further stocks were obtained from Calverton during the project period, to replenish numbers of a particular size class.

3.2.2. Grayling

The stock of small grayling was obtained from Calverton fish farm in the first summer. Large and medium fish were obtained from the wild, using electrofishing or angling. Fish were collected from the River Itchen, Test, Wylye and Avon throughout the duration of the project, as they suffered heavy mortailites in captivity. Some of the small, hatchery-reared grayling grew sufficiently to be included in the medium size category in later tests.

3.2.3. Eels

The eels were obtained by electrofishing from the Rivers Adur, Thames, Taff, Meon, and Severn tributaries throughout the duration of the project.

3.2.4. Bream

Bream were obtained at the beginning of the project from Calverton fish farm and Moore and Moore Carp hatcheries.

3.3   Fish husbandry

The unheated stock tanks were situated outside, and were consequently subject to natural diel and seasonal temperature fluctuations. Although the tanks were fitted with solid lids to prevent the fish from jumping out, these were not flush fitting and small gaps were left to allow light to penetrate, thus maintaining the natural day/night cycle. Artificial weed and plastic pipes were added to provide the fish with cover, with the aim of reducing stress. The stock fish were fed daily, and the water in the tanks was changed by partial replacement (normally 30% daily). During warmer weather, the water in tanks housing diseased or thermally sensitive fishes (such as grayling) was changed twice a day, to minimise the concentrations of any free swimming stages of pathogens, and to reduce water temperatures. On a monthly basis, fish from each stock tank were placed in a temporary container and the whole tank was drained, stripped, and disinfected with either a peroxide based (Hyperox) or an iodophor (FAM 30) disinfectant. Where space allowed, tanks were left fallow to desiccate resistant life stages of parasites.

Food was either pelleted (trout and / or carp pellets) or live (maggots and / or 'pinkies') according to the fish's preference. Eels were additionally fed chopped earthworms. Pellet was normally fed by hand, and a drip feeder was used for live foods. Drip feeders reduced the lifting of tank lids and movement around the tank, and were particularly suitable for the sensitive grayling. Internal electric pumps provided a constant low-velocity circulation of water within the tank, in order to exercise the fish, with the exception of bream. The bream were exercised for a 2-hour period twice a day, as a continuous flow in the tank was too strong, and the fish became exhausted. Nets were disinfected after each use, other equipment such as buckets and bags used for transportation were rinsed between uses, and disinfected periodically.

Health checks were carried out on a weekly basis, where a sample of fish was removed from the stock tank and examined closely for wounds, signs of disease and parasites. If any symptoms were present, the whole tank was treated, and fish were closely monitored until recovery. Outbreaks of whitespot (*Ichthyophthirius multifiliis*) affected all species during the project. Eels were also affected by other parasites, notably *Anguillicola*, *Dactylogyrus* and *Gyrodactylus,* which are present in the wild, but infestations were accentuated due to the close proximity of other eels in the tanks. *Dactylogyrus* and *Gyrodactylus* were successfully eradicated by increasing the salinity of the tank water to full strength seawater (Salinity > 30 ‰).

Virtually all of the grayling collected from the wild developed disease or infection after a period in captivity. The most common symptoms were red, open sores on the flanks, bleeding fins and raised scales. The problems were most prevalent at high temperatures, and appeared to be exacerbated by handling and testing, however even grayling that were not tested developed symptoms. Neither the source, nor method of capture appeared to influence the occurrence of disease in grayling. Samples of diseased grayling were taken

to a laboratory for analysis, but the results were inconclusive. Farmed grayling were held and tested separately from wild stocks and did not develop any symptoms for several months.

Bream and barbel were also affected by bacterial infections, but responded well to treatment, and generally remained healthier than the wild grayling stocks.

3.4   Swimming Test Apparatus

Swimming test apparatus was essentially the same as used during Phase 1 of the project.

3.4.1   The high-speed tunnel

The high-speed tunnel was designed and constructed specifically for Phase 1 of this project (Clough *et al.*, 2000), and was used to test burst-swimming capacity. The maximum achievable velocity was of the order of 4m s^{-1}. The tunnel itself was self-contained and consisted of a variable recirculating water system and reservoir (Figure 3.1). The swimming chamber was 1.5m long x 0.25m x 0.25m, and had a plexiglass viewing panel. An access port for fish introduction was provided at the top, and an instrument port. Water flow was generated by an electronically regulated pump and was controlled by valves with lockable settings. Using these controls, speed could be continuously adjusted to a resolution of ~0.1% of the overall range. Water velocity through the flume was measured using a calibrated Streamflo® high-speed probe (Nixon Instrumentation Ltd) and readout unit located in the downstream end of the test section. In normal use the probe was positioned to measure water velocity in the centre of the tunnel, but a study of the distribution of water velocities at different depths was also carried out.
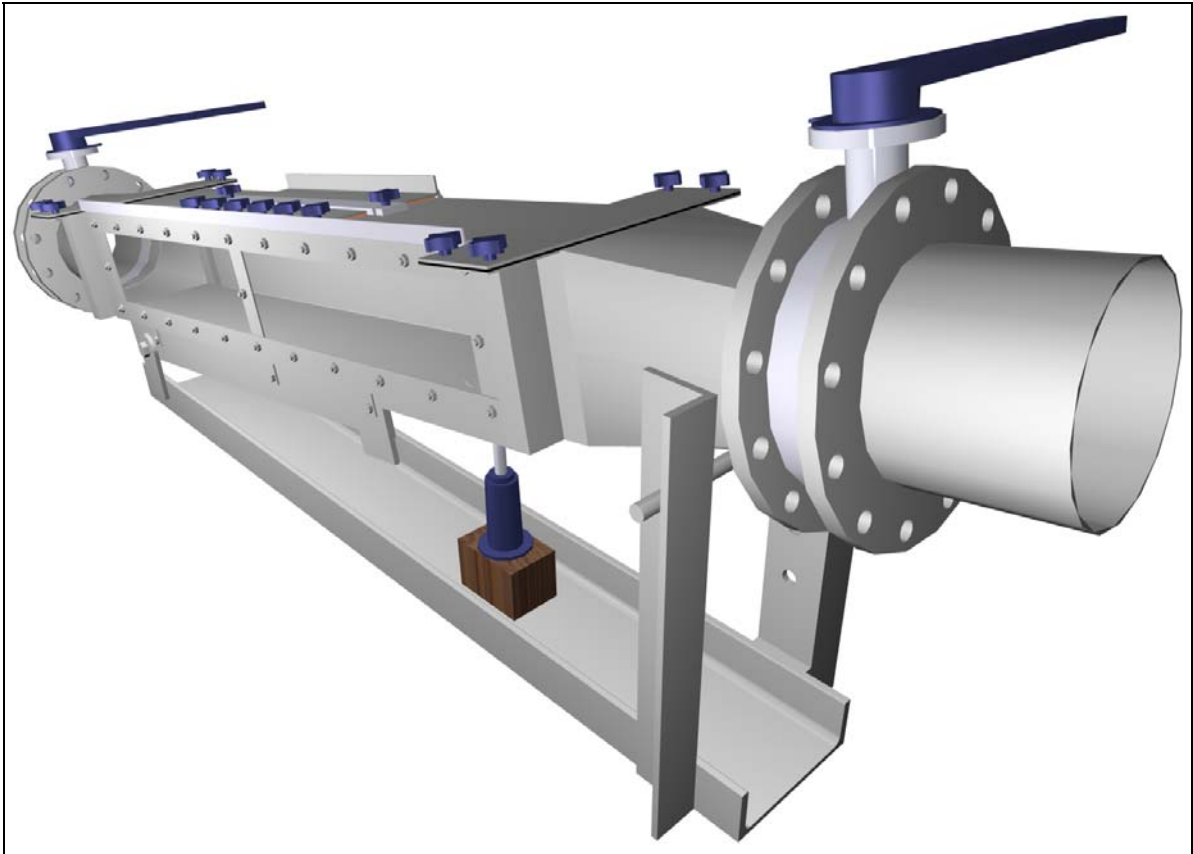
Figure 3.1. **Three-dimensional rendering of the high-speed tunnel test section, showing window at front, access hatch at top and tilting arrangement. The swimming chamber is 1.5m long x 0.25m x 0.25m. The figure shows the tunnel in the raised position, but the burst swimming tests were carried out with the tunnel in the horizontal position.**

3.4.2 The low-speed flume

The low speed flume was used to test the sustained swimming capacity of the barbel, grayling, eels and bream. The general hydraulic characteristics have been described by Turnpenny and Bamber (1983). The flume tank was oval, with a long axis of approximately 8m, and speeds up to 2.0m s^{-1} could be generated in the test section (Figure 3.2). The test section of the flume was divided up into four equal length compartments using 10mm wire mesh screens, each compartment being 1m long by 0.6m wide. Plastic mesh screens (5mm squares) were added for smaller size classes of fish. Water flow around the low-speed flume was governed by an electronically controlled propeller. Flow-straightening vanes, mesh panels and "honeycomb" panels at the entrance to the test section ensured water flow through the test section was uniform. Water velocity was measured in the test sections using a calibrated low-speed Streamflo® (Nixon Instrumentation Ltd) probe and readout unit. The water depth and velocity in each of the four test sections was not the same, but became slightly shallower and faster in a downstream direction as a result of the head loss across each screen. Velocity through the sections was measured at the end of each test.
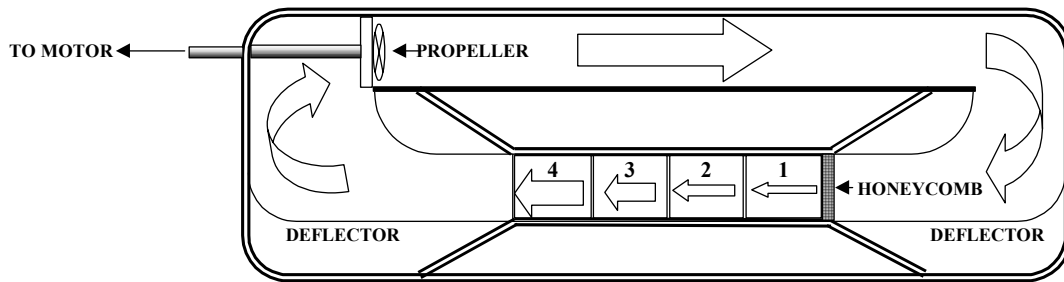
Figure 3.2. Diagram of the low-speed flume. Arrows show direction of water flow, width of arrows within the test section denotes progressively increasing velocities.

3.4.3   The eel flume-box

The swimming capacity of small and medium eels needed to be tested in a specially constructed flume-box, due to the tendency of eels to escape from the low speed flume. The flume box was constructed using a plastic box measuring 270 x 130mm (Figure 3.3). Both ends were open and covered with a net screen (mesh size 3mm). This flume-box was positioned into the flow of the burst flume, suspended from the access port. Eels were placed inside the box and swam for 200 minutes as normal. The water velocity inside the eel flume box was measured with a calibrated Streamflo® high-speed probe (Nixon Instrumentation Ltd) flow meter. The sides and base of the eel flume box were smooth plastic and boundary layer effects were minimal.
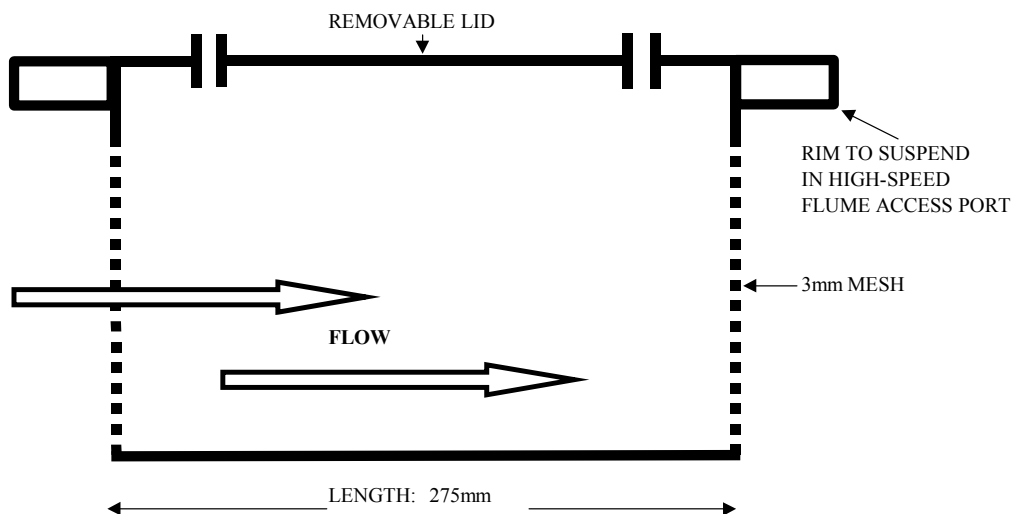
Figure 3.3. Diagram of the eel flume-box. Arrows indicate the direction of water flow.

3.5   Swimming Test Protocols

3.5.1   High-speed tunnel protocol

Burst swimming experiments were carried out in the high-speed tunnel. Prior to testing, the fish were acclimated for at least 24 hours in tanks connected to the reservoir of the high speed tunnel. The tunnel was operated for at least five minutes prior to the start of the first test to ensure the water was fully aerated, and the water temperature in the tunnel was recorded at the start and end of each test. The smooth glass base and sides of the flume

ensured that boundary layer effects were minimised. Each fish was carefully introduced to the tunnel to minimise handling stress, with the water flowing at approximately 1-1½ body lengths per second. The fish was allowed to acclimatise to swimming at this speed for 5-10 minutes. After the acclimation period had elapsed the speed was increased to $0.8m s^{-1}$, and the stopwatch was started (N.B. if the fish had been acclimatised at $0.4m s^{-1}$, the speed was increased to $0.6m s^{-1}$ for twenty seconds, and then to $0.8m s^{-1}$ after this). After 20 seconds at $0.8m s^{-1}$, the speed was increased to $1.0m s^{-1}$. After a further 20 seconds, the speed was increased to $1.1m s^{-1}$ and so on, with subsequent increases of $0.1m s^{-1}$ occurring at 20 second intervals. As soon as each fish dropped back against the screen the water flow was stopped, and the time recorded. The fish were then removed from the tunnel and returned to a stock tank within the temperature controlled room. Critical burst swimming speed (CBSS) was calculated assuming a gradual increase in speed i.e. a $0.5cm s^{-1}$ increase with each second, in accordance with standard CBSS methodology (Brett, 1967). For example a 150mm fish achieved speeds of $0.8m s^{-1}$, $1.0m s^{-1}$ and $1.2m s^{-1}$ for 20 seconds but at $1.4m s^{-1}$ it was able to swim for only for 11 seconds. The CBSS was then calculated as the speed at which the full 20s was swum, plus $11/20^{ths}$ of the velocity increment ($0.2m s^{-1}$), i.e.:

$$CBSS = 1.2 + (11/20 \times 0.2) = 1.31m s^{-1} = 8.73 bl s^{-1}.$$

3.5.2   Low-speed flume protocol

Fish were tested in batches of up to 45 individuals. A settling period of 2 hours was allowed before the start of each endurance-swimming test. This settling period allowed the fish to recover from any handling stress sustained during capture from the stock tanks, and to acclimatise to their new surroundings. During the settling period water velocity was set at around one body-length per second, and for large eel tests the channel was covered to prevent the fish climbing out. After the settling period, the water velocity was increased gradually up to the test speed. The start of the experiment was taken as the point at which the test speed was reached, and any fish exhausted prior to this were removed and recorded as "Time = 0". Each endurance test lasted for 200 minutes. As each fish became exhausted it was removed from the flume, measured and the time recorded. The fish was returned to the stock tank as soon as possible after being removed from the flume. After 200 minutes, the water flow was slowed to a stop, and the water temperature recorded. All remaining fish were measured, with any damage to fins being recorded.

3.5.3   Eel box protocol

The endurance speed of medium and small eels was tested in the high speed flume using the specially designed eel box. The endurance speed of the large eels was tested using the low speed flume. Small and medium eels were tested in batches of around 10 individuals due to the small size of the compartment. The experiments were carried out in the same way as the endurance tests in the low speed flume. Water velocities were measured at the end of each test.

4.   RESULTS

Burst and endurance swimming speed tests were carried out with all test species, in each of the required temperature categories. In total more than 9,800 fish observations were made in endurance trials, with in excess of 1,300 in burst trials.

4.1   Endurance swimming

Endurance swimming charts show the median endurance time attained by fish in swimming trials, at a range of water velocities, expressed in metres per second (Figures 4.1.1 to 4.1.3). The error bars show the position of the upper and lower quartiles of endurance time. In addition, an exponential trendline has been fitted to median endurance times using the trendline function in the Excel package. The trendlines are included for clarity, and show the relationship between median endurance time and water velocity. Equivalent charts, also showing the median endurance times of fish at a range of test velocities are given in the appendix, with the test velocities being expressed in fish body lengths per second (APPENDIX II, Figures AII.1a to AII.3j).

Barbel

The endurance swimming capacity of barbel generally increased with increasing length, and this pattern was consistent in each of the temperature bands (Figs 4.1.1a-c, 4.1.2a-c & 4.1.3a-c). The overall effect of temperature was less noticeable, and results in each of the two lower temperature categories were similar (Figs 4.1.1a-c & 4.1.2a-c). Performance was however noticeably better in the $>15^{o}$C category (Fig 4.1.3a).

Grayling

The performance of grayling in endurance swimming trials also shows a general increase with increasing body length in each of the temperature categories. Increasing the test temperature from 5-10 to 10-15°C resulted in an improvement in performance (Figs 4.1.1d-f & 4.1.2d-f), however a further increase in temperature to $>15^{o}$C appears to result in an overall reduction in the endurance swimming capacity of grayling (Figs 4.1.3 d-f).

Eel

Eels were not tested within the lowest temperature category, and small and medium eels showed equivalent performance in each of the temperature categories tested (Figs 4.1.2g-i & 4.1.3g-i). Large eels, on the other hand, showed a noticeable improvement in performance at the highest temperature (Figs 4.1.2g-i & 4.1.3g-i). Although endurance swimming performance was generally poor compared with that of the other species tested, eels did show a general improvement with increasing length in both temperatures.

Bream

Only one size of bream was tested, so the effect of length on endurance swimming can only be assessed within the narrow range of the length category. Large numbers of bream were tested, and there was a noticeable increase in performance with increasing temperature (Figs 4.1.1g, 4.1.2j & 4.1.3j).

4.1.1 Endurance at 5-10°C
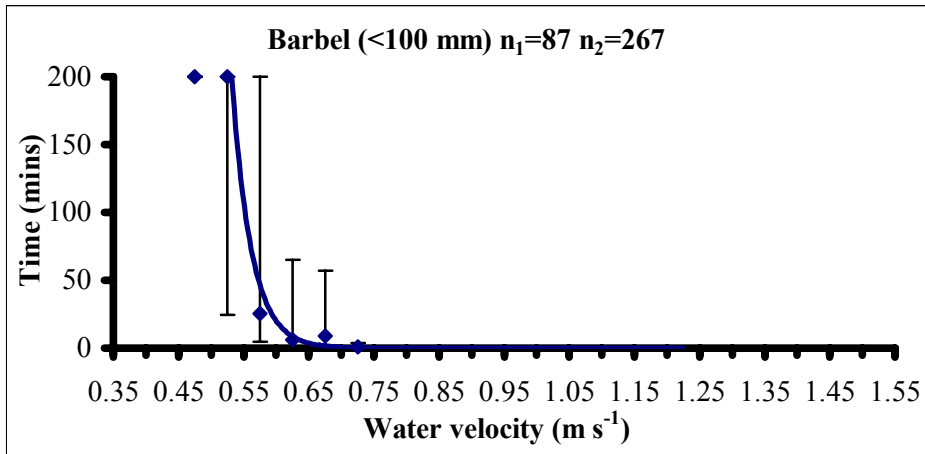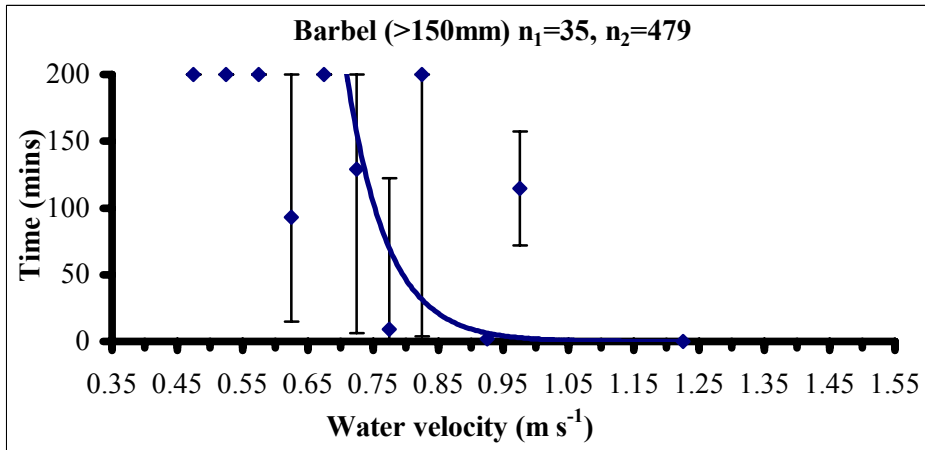

Figure 4.1.1a
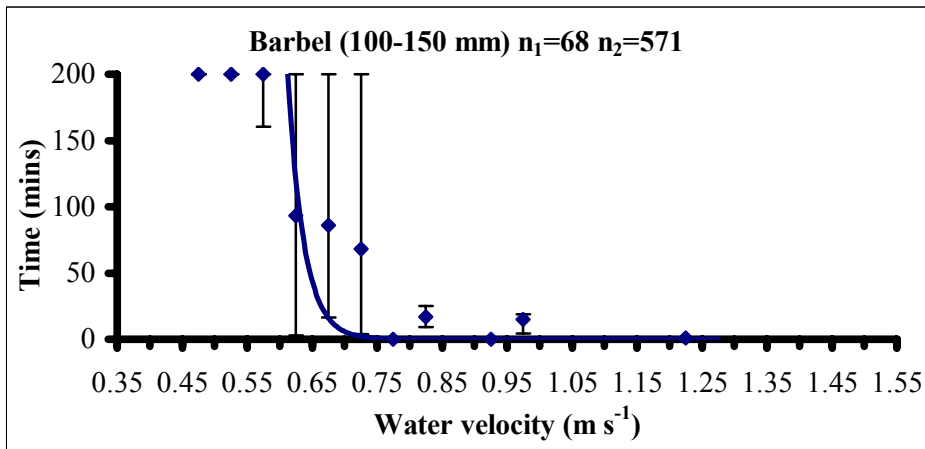
Figure 4.1.1b

Figure 4.1.1c

Figures 4.1.1a-c. Endurance results for barbel at 5-10°C. Error bars show upper and lower quartiles. n_1 = no. of individual fish tested; n_2 = total no. of fish tested. Exponential trendline added.
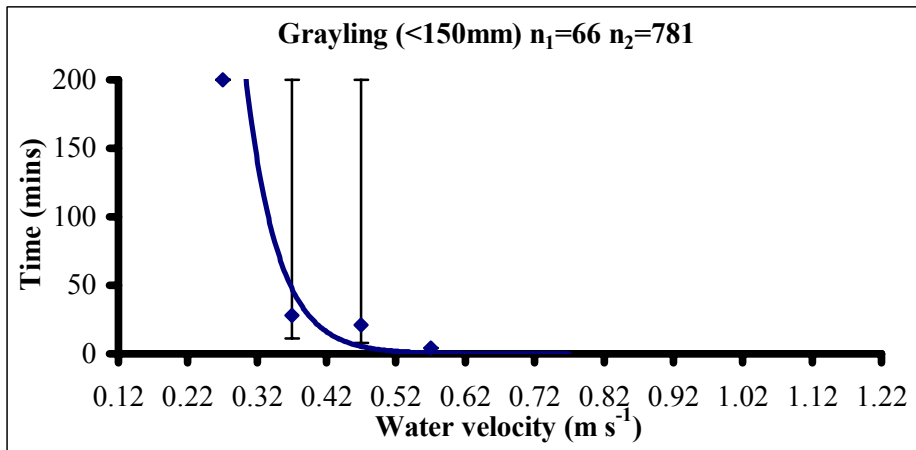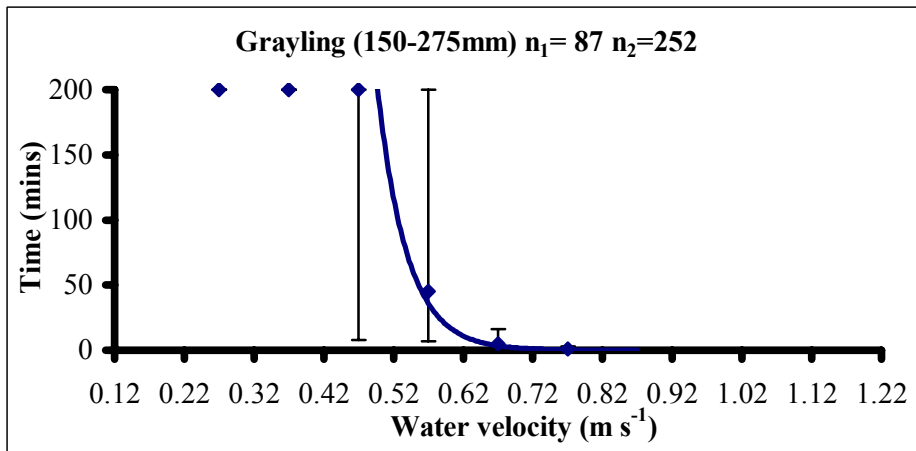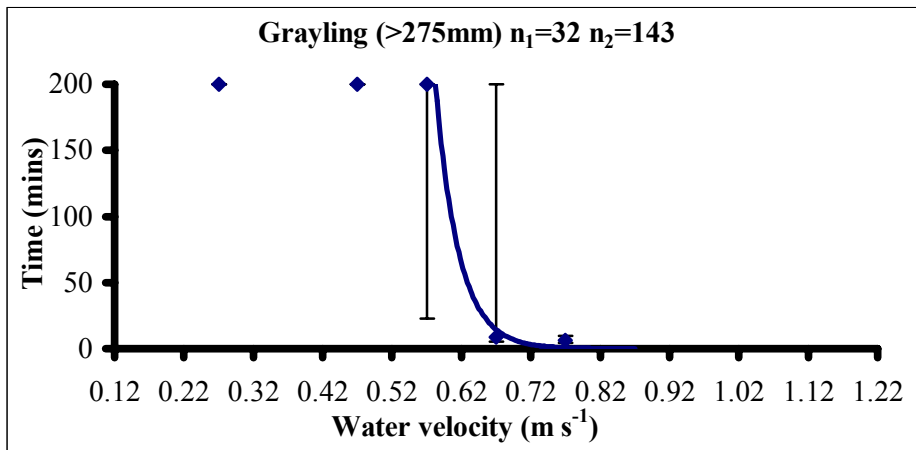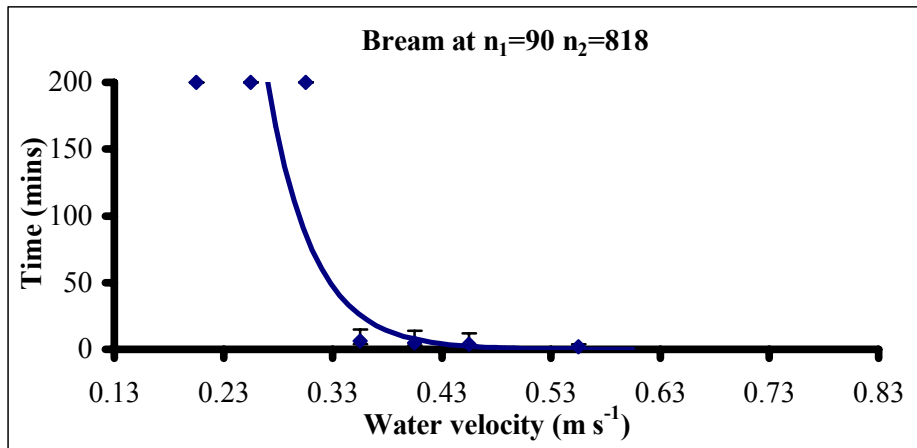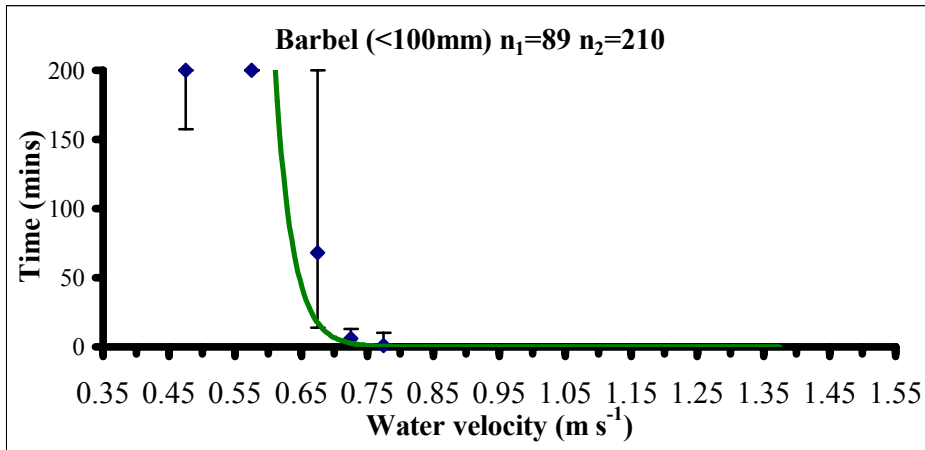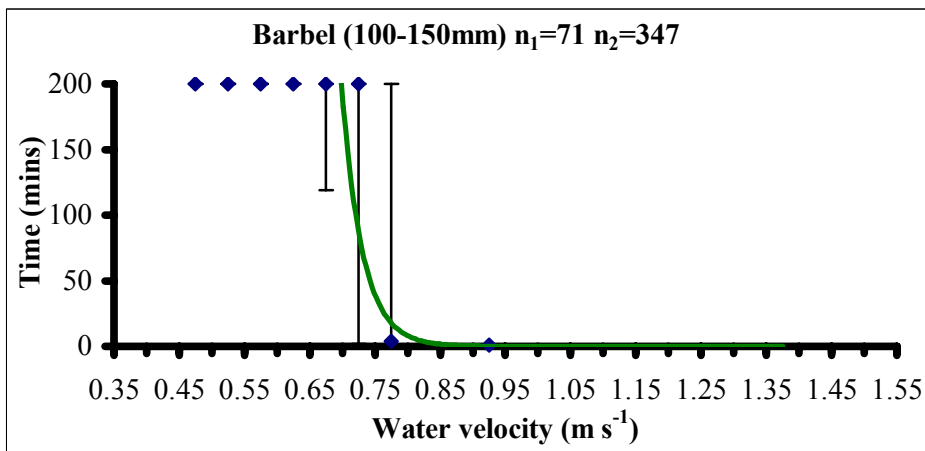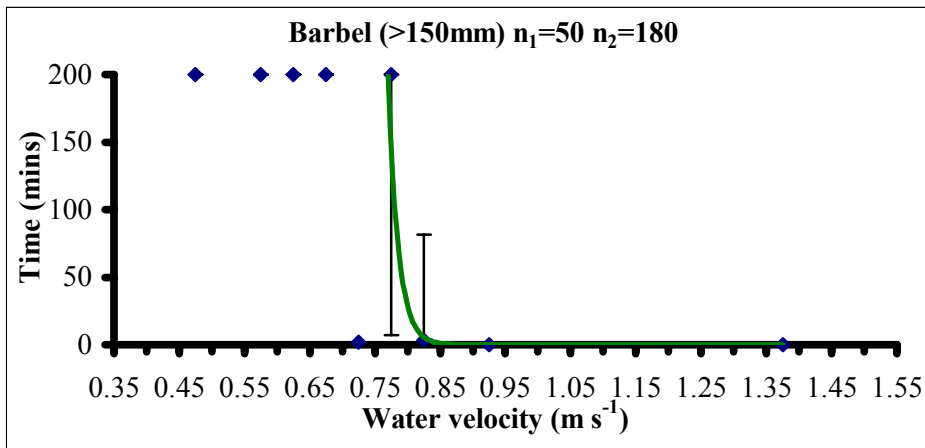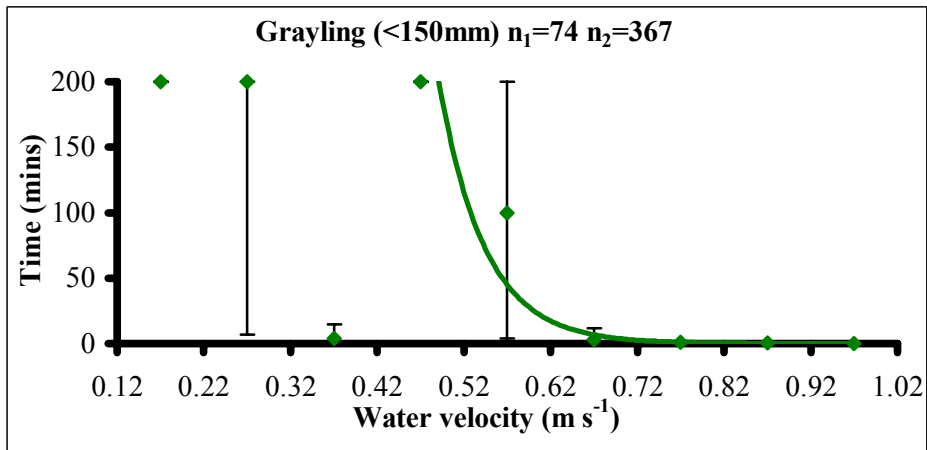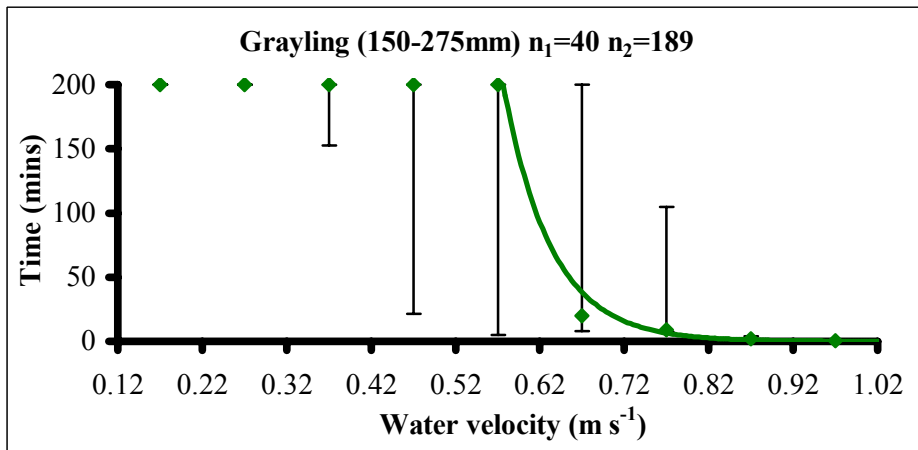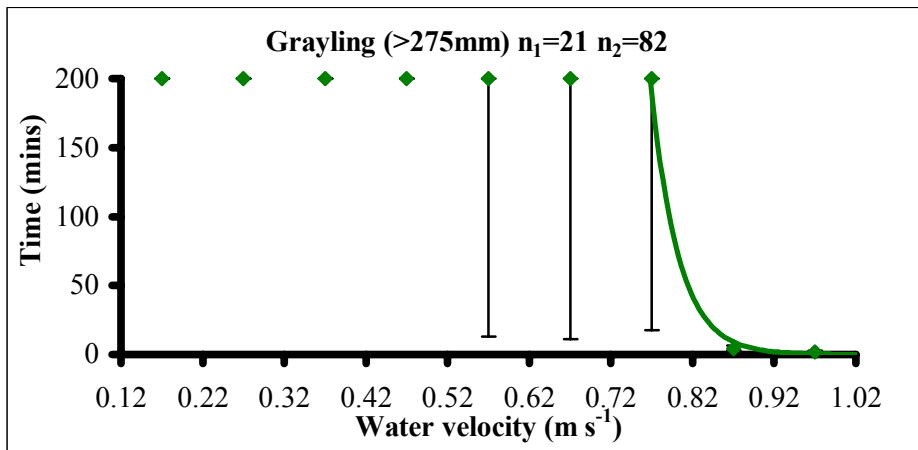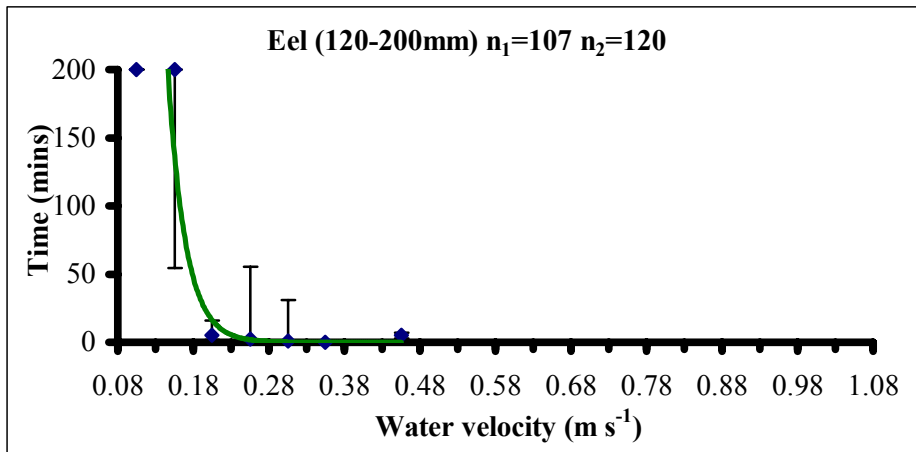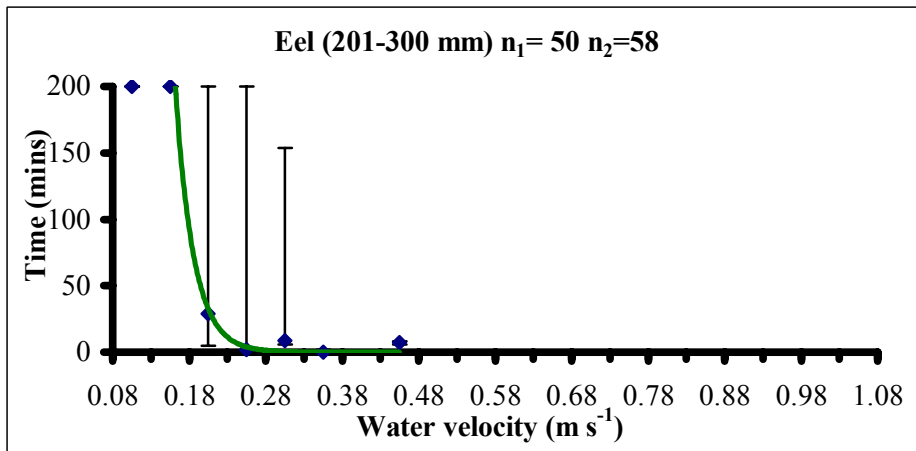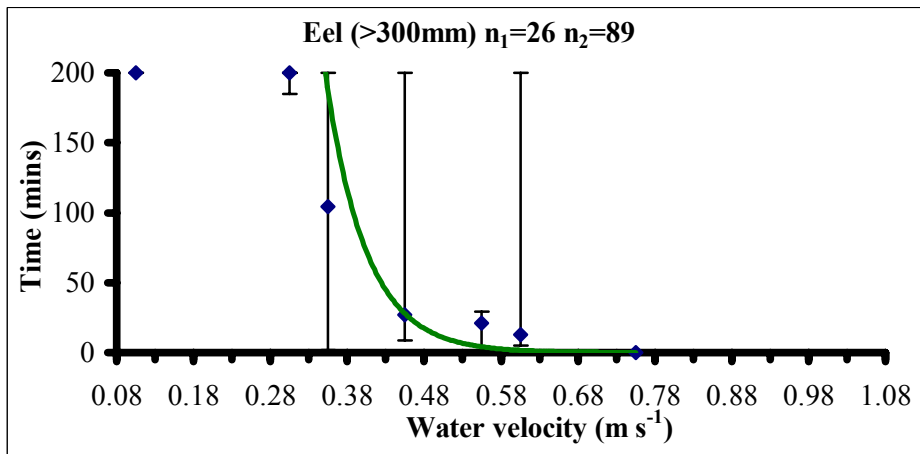
Figure 4.1.1d

Figure 4.1.1e

Figure 4.1.1f

Figures 4.1.1d-f. Endurance results for grayling at 5-10°C. Error bars show upper and lower quartiles. n_1 = no. of individual fish tested; n_2 = total no. of fish tested. Exponential trendline added.
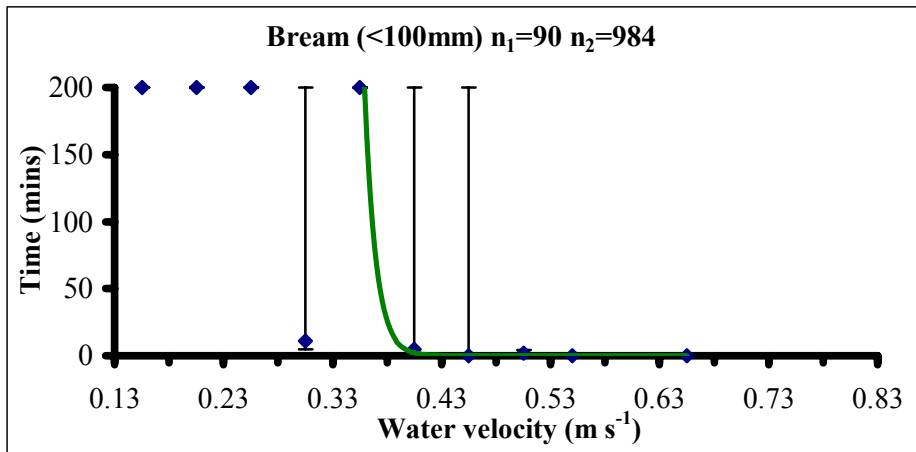
Bream at n_1=90 n_2=818

Figure 4.1.1g

Figures 4.1.1g. Endurance results for bream at 5-10°C. Error bars show upper and lower quartiles. n_1 = no. of individual fish tested; n_2 = total no. of fish tested. Exponential trendline added.
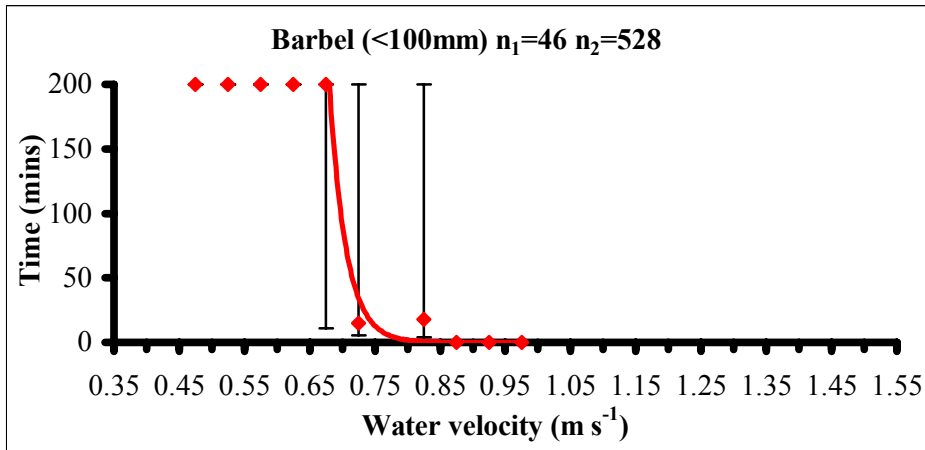
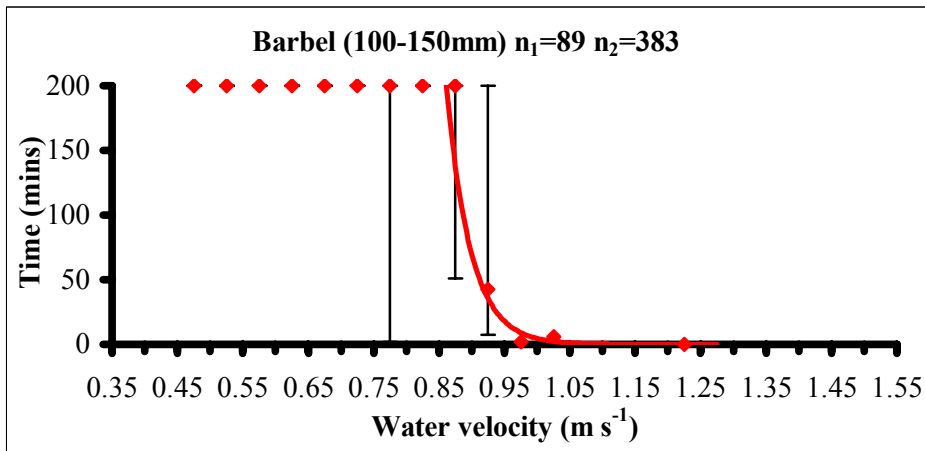## 4.1.2   Endurance at 10-15°C

Figure 4.1.2a
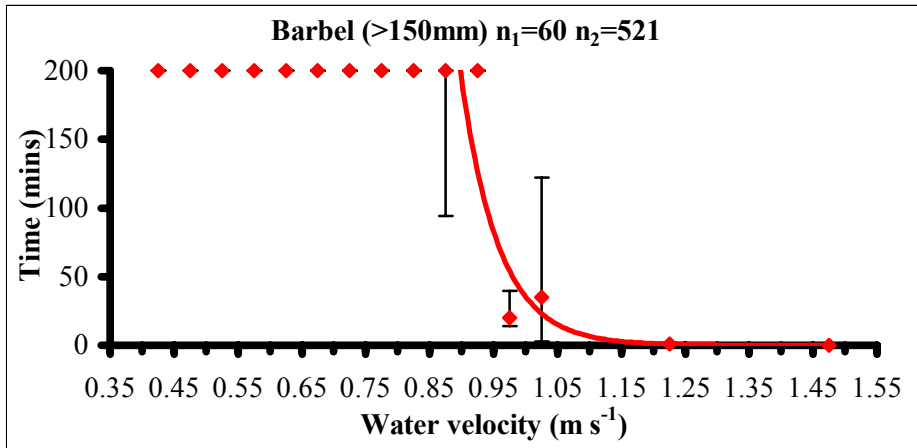

Figure 4.1.2b

Figure 4.1.2c

Figures 4.1.2a-c.   Endurance results for barbel at 10-15°C. Error bars show upper and lower quartiles. n_1 = no. of individual fish tested; n_2 = total no. of fish tested. Exponential trendline added.

Figure 4.1.2d

Figure 4.1.2e

Figure 4.1.2f

Figures 4.1.2d-f. Endurance results for grayling at 10-15°C. Error bars show upper and lower quartiles. n_1 = no. of individual fish tested; n_2 = total no. of fish tested. Exponential trendline added.
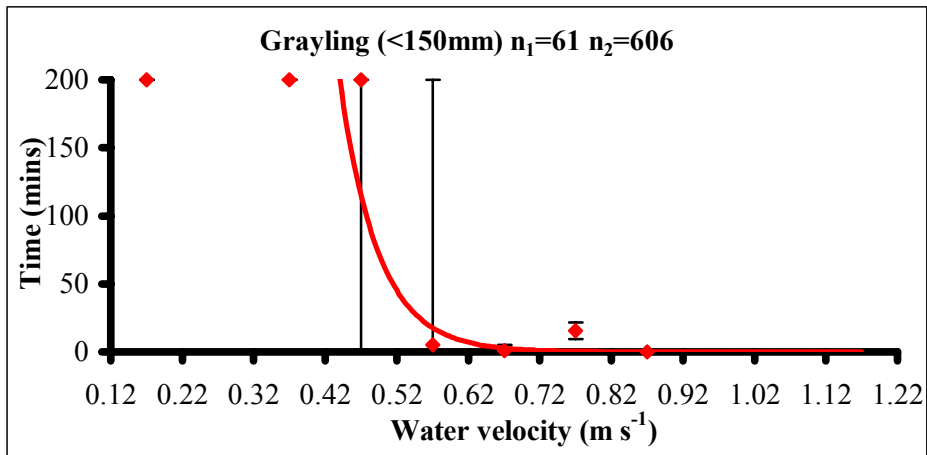
Figure 4.1.2g

Figure 4.1.2h

Figure 4.1.2i

Figures 4.1.2g-i. Endurance results for eels at 10-15°C. Error bars show upper and lower quartiles. n_1 = no. of individual fish tested; n_2 = total no. of fish tested. Exponential trendline added.
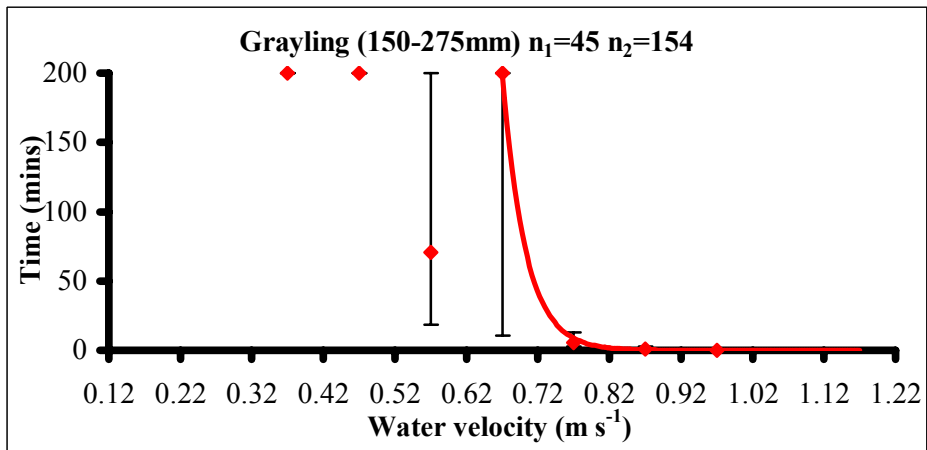
Bream (<100mm) n_1=90 n_2=984

Figure 4.1.2j. Endurance results for bream at 10-15°C. Error bars show upper and lower quartiles. n_1 = no. of individual fish tested; n_2 = total no. of fish tested. Exponential trendline added.
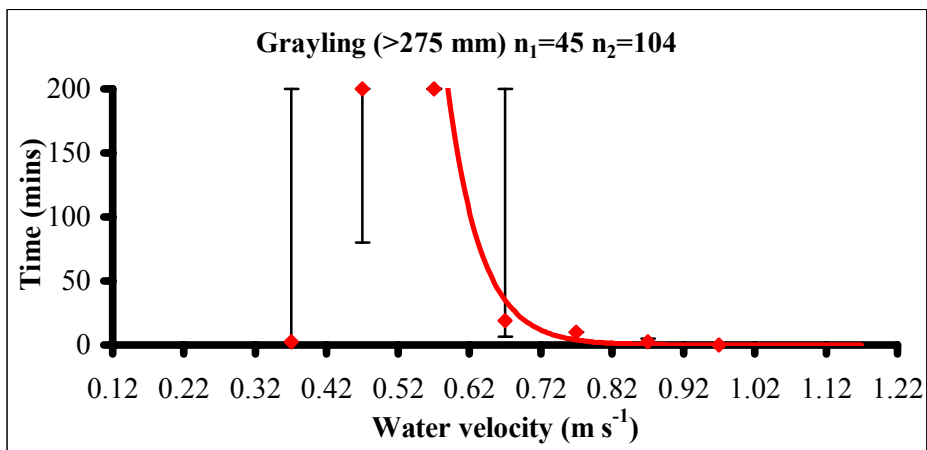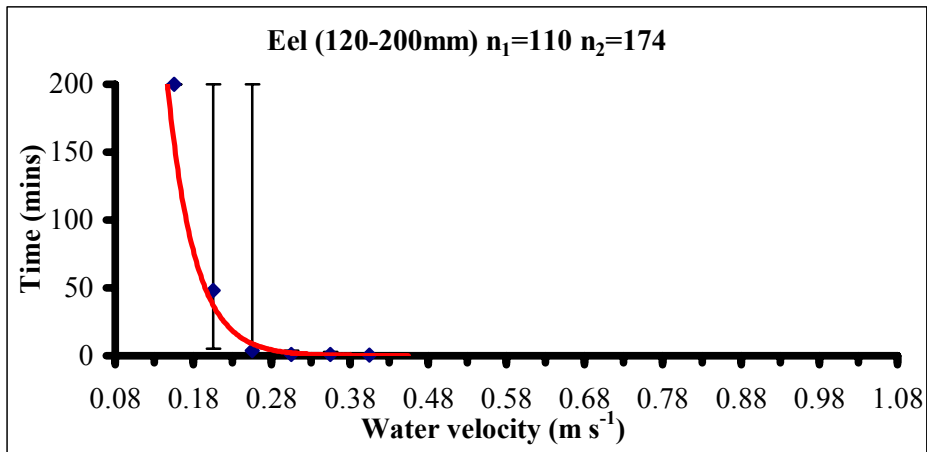
4.1.3 Endurance at 15-20°C

Figure 4.1.3a

Figure 4.1.3b

Figure 4.1.3c

Figures 4.1.3a-c. Endurance results for barbel at >15°C. Error bars show upper and lower quartiles. n_1 = no. of individual fish tested; n_2 = total no. of fish tested. Exponential trendline added.
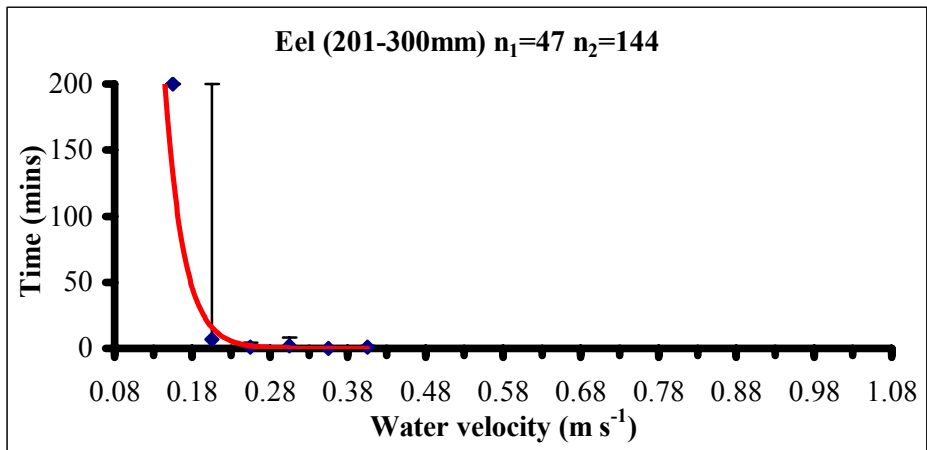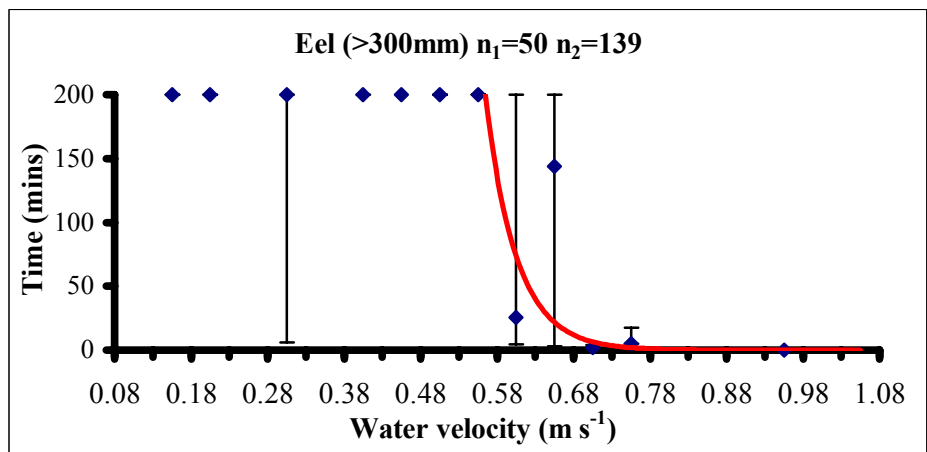
Figure 4.1.3d

Figure 4.1.3e

Figure 4.1.3f

Figures 4.1.3d-f. Endurance results for grayling at >15°C. Error bars show upper and lower quartiles. n_1 = no. of individual fish tested; n_2 = total no. of fish tested. Exponential trendline added.
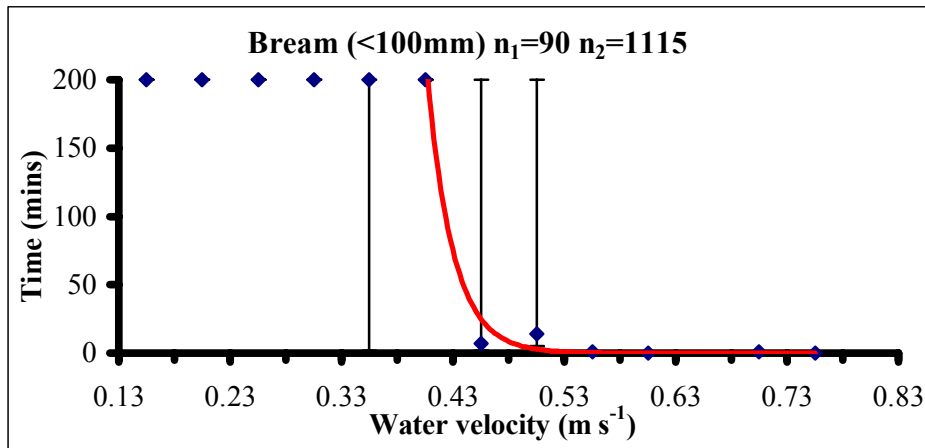
Figure 4.1.3g

Figure 4.1.3h

Figure 4.1.3i

Figures 4.1.3g-i. Endurance results for eels at >15°C. Error bars show upper and lower quartiles. n_1 = no. of individual fish tested; n_2 = total no. of fish tested. Exponential trendline added.

Figure 4.1.3j

Figures 4.1.3j. Endurance results for bream at >15°C. Error bars show upper and lower quartiles. n_1 = no. of individual fish tested; n_2 = total no. of fish tested. Exponential trendline added.
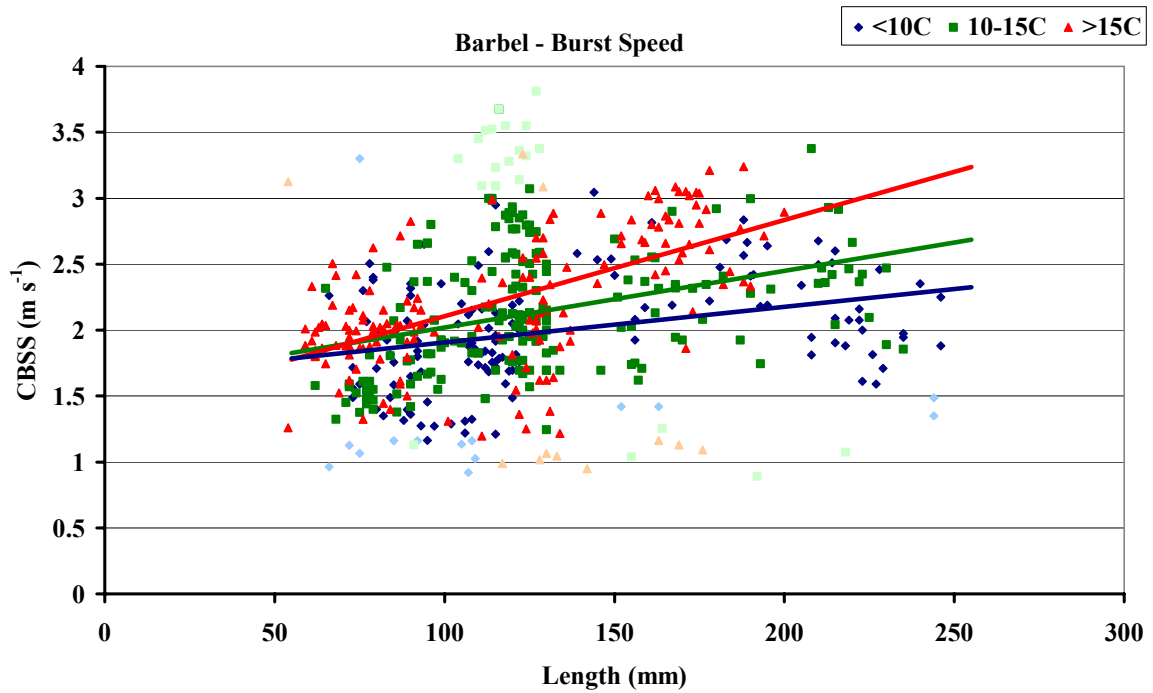
4.2 Burst swimming

Scatter plots showing CBSS against fish length are given in Figures 4.2a-d. The results from each temperature are plotted in a different colour. Linear trendlines were generated for each temperature category using the statistical functions in MS Excel.

It was noticed in burst swimming trials that occasionally fish would become caught on the downstream screen very early during the test, and that they were unable to escape from the screen due to the pressure exerted by the water flow. It was considered that these fish had not reached the limit of their swimming ability, and that the CBSS value achieved would not be a true reflection of their capability. In addition, a small number of the fish tested exhibited a form of cheating, where by wedging themselves into the angle of the flume, and angling their pectoral fins they were able to hold position, without actively swimming. It was considered that the CBSS values assigned to these fish did not offer a true reflection of the swimming ability of that species. To this end, the results assigned to fish that were considered not to be a true reflection of their swimming ability were excluded from the multiple regression analysis (Tables 4.2a-d). For completeness, however, these data are displayed on the relevant charts (Figures 4.2a-d), and can be distinguished from those data used in the regression as they are plotted in a paler colour.

4.2.1 Barbel

The critical burst swimming performance of barbel shows a general increase with both increasing fish length, and temperature (APPENDIX III, Figs AIII.1a-c, AIII.2a-c & AIII.3a-c). The notable exception to this general trend being the higher than expected performance of the medium sized barbel, in the 10-15°C category (Fig. AIII.2b). In order to examine the critical burst swimming performance of barbel as a whole, the data for each size class and temperature were plotted on the same axes (Fig. 4.2a), and a multiple regression of CBSS against fish length (L) and temperature (T) was calculated (Table 4.2a). P-values of <0.0001 show the length and temperature coefficients differ highly significantly from unity.

Figure 4.2a. **Critical burst swimming speeds of barbel in three temperature categories.**

Table 4.2a. Summary output from multiple regression analysis for barbel.

Regression Statistics	
Multiple R	0.509
R Square	0.259
Adjusted R Square	0.256
Standard Error	0.391
Observations	467

ANOVA

	df	SS	MS	F	Significance F
Regression	2	24.835	12.418	81.254	5.5612E-31
Residual	464	70.910	0.153		
Total	466	95.745			

	Coefficients	Standard Error	t Stat	P-value	Lower 95%	Upper 95%
Intercept	-1.791	0.308	-5.817	0.000	-2.396	-1.186
LN (T)	0.423	0.059	7.147	0.000	0.307	0.540
LN(L)	0.593	0.053	11.226	0.000	0.490	0.697

4.2.2 Grayling

As with the endurance swimming tests, grayling showed a generally improved performance with increasing fish size in burst swimming trials (APPENDIX III Figs AIII.1d-f, AIII.2d-f & AIII.3d-f). It was also noticeable that performance was reduced in the highest temperature category (Figs AIII.3d-f). Critical burst swimming data for each size class and temperature were plotted together (Fig. 4.2b), and a multiple regression of CBSS against fish length and temperature was calculated (Table 4.2b). A P-value of <0.0001 shows that the length coefficient differs highly significantly from unity, while that for temperature was non-significant (P>0.05).
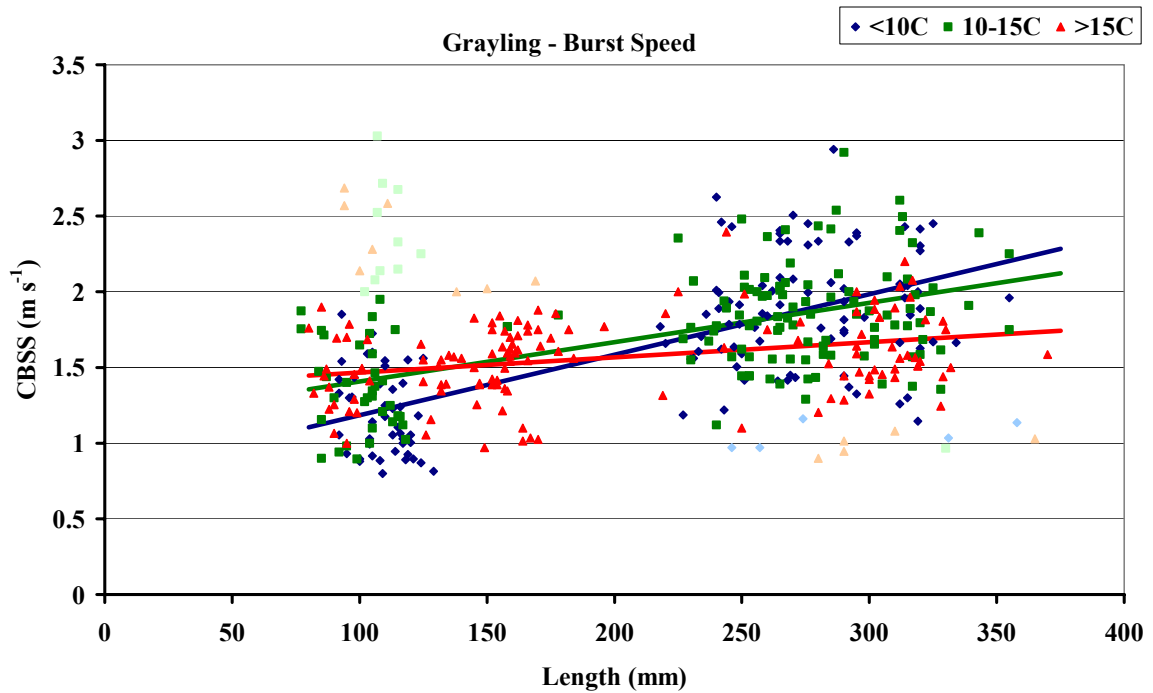
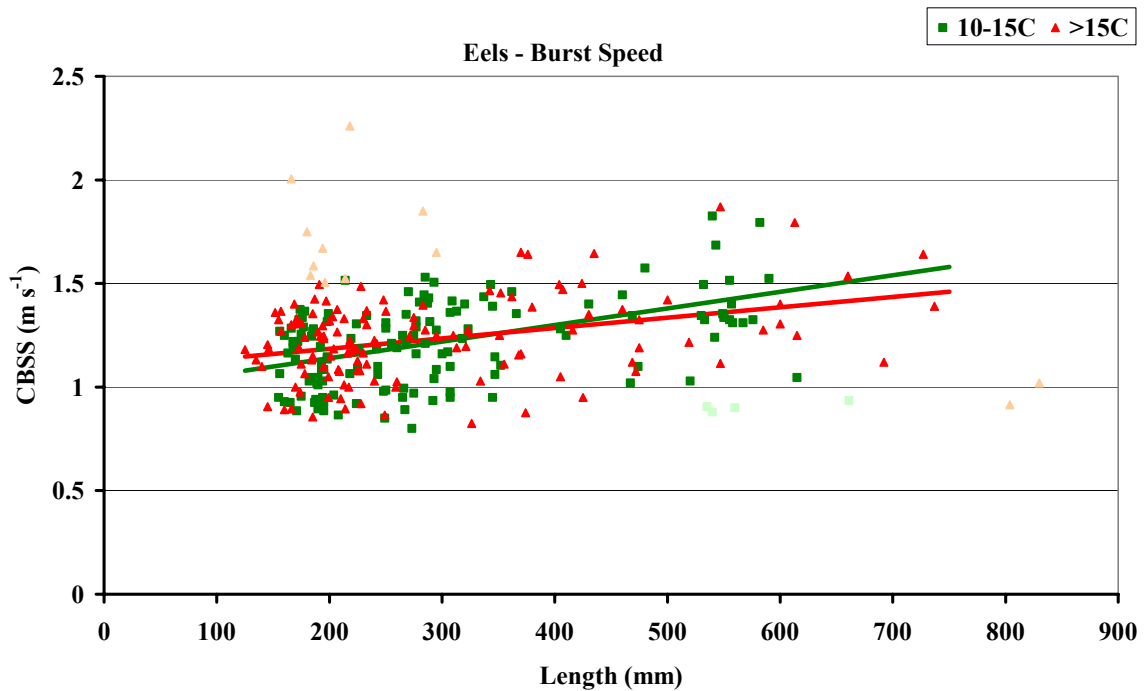**Figure 4.2b. Critical burst swimming speeds of grayling in three temperature categories.**

Table 4.2b. Summary output from multiple regression analysis for grayling.

Regression Statistics	
Multiple R	0.567
R Square	0.321
Adjusted R Square	0.318
Standard Error	0.323
Observations	394

ANOVA

	df	SS	MS	F	Significance F
Regression	2	19.315	9.658	92.516	1.26848E-33
Residual	391	40.816	0.104		
Total	393	60.131			

	Coefficients	Standard Error	t Stat	P-value	Lower 95%	Upper 95%
Intercept	-0.683	0.242	-2.818	0.005	-1.159	-0.206
LN (T)	-0.083	0.054	-1.530	0.127	-0.190	0.024
LN(L)	0.482	0.036	13.390	0.000	0.411	0.553

4.2.3 Eel

The burst swimming capacity of eels was generally low compared with the other species, and showed little increase with increasing length (APPENDIX III, Figs AIII.2g-i, AIII.3g-i). Burst swimming performance does appear to be slightly improved within the highest temperature category (Figs AIII.3g-i). The critical burst swimming speeds for each size class and both temperatures were plotted together (Fig. 4.2c), and a multiple regression of CBSS against fish length and temperature was calculated (Table 4.2c). A P-value of <0.0001 shows that the length coefficient differs highly significantly from unity, while that for temperature was non-significant (P>0.05)
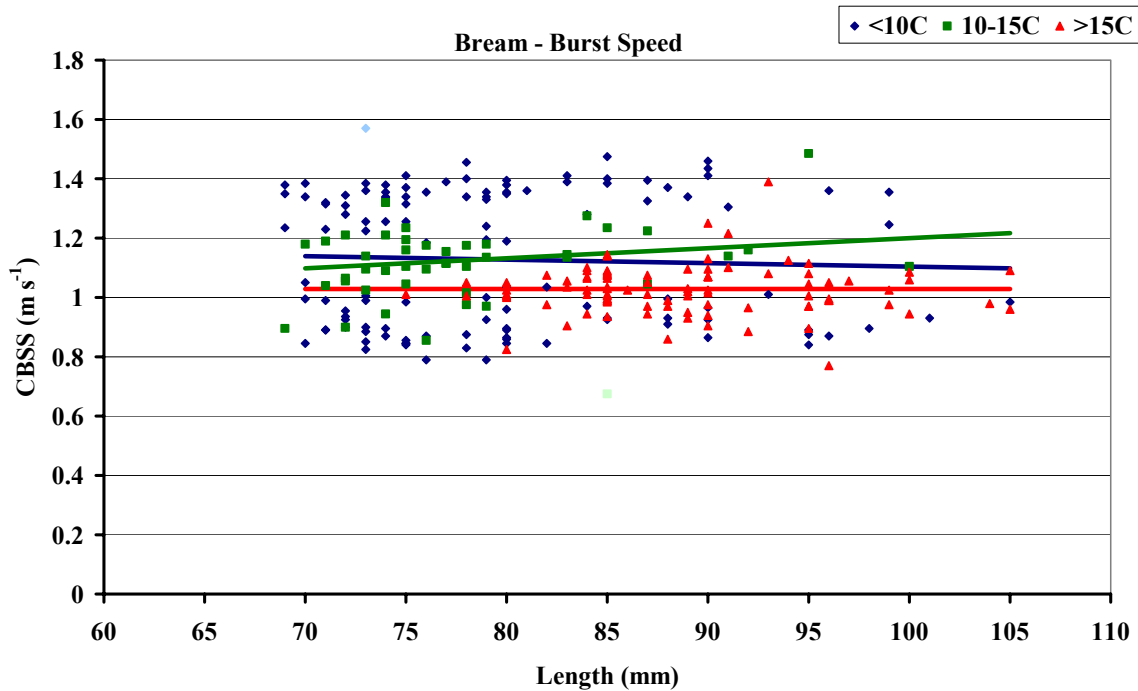

Figure 4.2c. Critical burst swimming speeds of eels in two temperature categories.

Table 4.2c. Summary output from multiple regression analysis for eel.

Regression Statistics	
Multiple R	0.420
R Square	0.176
Adjusted R Squar	0.170
Standard Error	0.180
Observations	263

ANOVA

	df	SS	MS	F	Significance F
Regression	2	1.805	0.903	27.790	1.15425E-11
Residual	260	8.444	0.032		
Total	262	10.249			

	Coefficients	Standard Error	t Stat	P-value	Lower 95%	Upper 95%
Intercept	-0.087	0.195	-0.443	0.658	-0.471	0.298
LN (T)	0.072	0.044	1.618	0.107	-0.016	0.159
LN(L)	0.198	0.027	7.304	0.000	0.145	0.252

4.2.4 Bream

The burst swimming capacity of bream was unusual, as contrary to the endurance swimming results, there was a general decrease in performance with increasing temperature (APPENDIX III, Figs AIII.1g, AIII.2j & AIII.3j). The critical burst swimming speeds for all three temperatures were plotted together (Fig. 4.2d), and a multiple regression of CBSS against fish length and temperature was calculated (Table 4.2d). A P-value of <0.05 shows the temperature coefficient to be significantly different from unity but that for length was not significant (P>0.05) over this narrow length range of fish.

Figure 4.2d. **Critical burst swimming speeds of bream in three temperature categories.**

Table 4.2d. Summary output from multiple regression analysis for bream.

SUMMARY OUTPUT

Regression Statistics	
Multiple R	0.574
R Square	0.329
Adjusted R Square	0.322
Standard Error	0.171
Observations	198

ANOVA

	df	SS	MS	F	Significance F
Regression	2	2.806	1.403	47.825	1.258E-17
Residual	195	5.722	0.029		
Total	197	8.528			

	Coefficients	Standard Error	t Stat	P-value	Lower 95%	Upper 95%
Intercept	1.110	0.525	2.116	0.036	0.075	2.145
LN (T)	-0.420	0.045	-9.427	0.000	-0.508	-0.332
LN(L)	0.248	0.129	1.928	0.055	-0.006	0.501

5. DISCUSSION

5.1 Comments on endurance swimming tests

The modification to the endurance flume, replacing the paddle wheel with a propeller was beneficial and allowed finer control of test velocities to be achieved. This allowed testing to be concentrated on the velocities that provided the most information, i.e. sufficiently fast so that not all the fish could complete the full 200 minutes, but not so fast that all of the fish were carried onto the screens within a few minutes. This fine control and replicability, along with the large numbers of fish tested, ensured a robust data set, even when there was considerable variation in individual performance.

5.2 Comments on burst swimming tests

Occasionally fish became caught on the screens very early in the tests, often at speeds which experience suggested should have been well within their swimming ability. In other situations fish demonstrated a form of cheating behaviour, which allowed them to attain swimming speeds in excess of those that would be expected for fish that swam normally throughout the trial. The results from these fish are shown on the CBSS charts for completeness, however it was considered that by excluding them from the regression analysis, more realistic estimates of burst swimming would be attained.

During normal burst testing water velocity was recorded on the centreline of the tunnel. In order to examine the effects of depth on water velocity, a calibration was carried out by positioning the probe at different distances above the bottom of the flume.
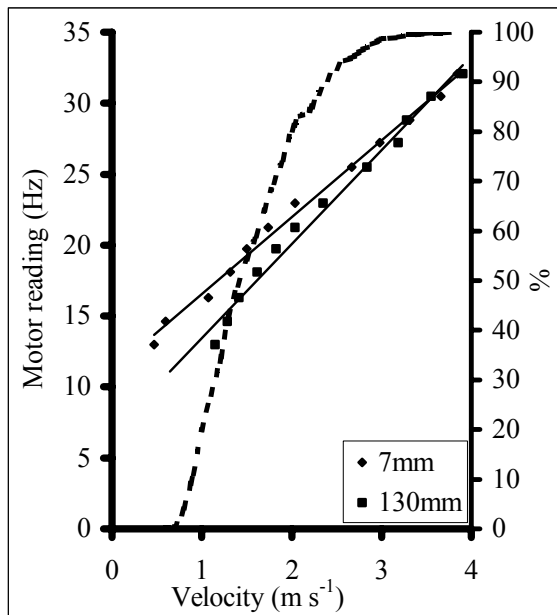
Figure 5.2a
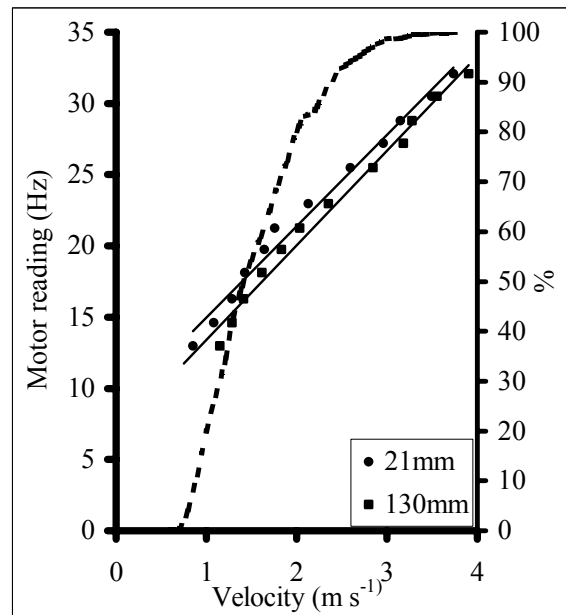
Figure 5.2b

Figures 5.2a&b. Charts showing the relationship between water velocity in the centre of the tunnel (130mm), and at 7mm & 21mm above the base respectively. The dotted line shows the cumulative percentage of fish attaining each velocity in all burst tests.

Measured water velocities at 7 & 21mm above the bottom of the tunnel were slower than in the centre of the tunnel, however it was noticeable that the magnitude of the difference

fell with increasing water velocity. The results show that when water velocity in the centre of the tunnel was approximately 2m s^{-1}, velocities at 7 and 21mm above the base of the tunnel were typically 15 & 14% lower respectively. At 3 m s^{-1} the difference fell to around 6 or 7%. Swimming behaviour varied between species and between individuals, however, in general terms the barbel tended to hug the base of the tunnel, while the other species tended to swim in the water column, often just above the base of the tunnel. The exact focal velocities experienced by these fish would, therefore, depend on their precise position. It is likely that fish hugging the bottom and those swimming in the water column just above the bottom would experience focal velocities similar to those measured at 7 and 21mm respectively. The surfaces of the high speed water tunnel were designed to be as smooth as possible, in order to minimise the effect of the boundary layer, and as such are at least as smooth as could be found anywhere in the field. Consequently, when applying the burst swimming data to the field situation, providing water velocities are recorded using standard methodologies (i.e. at 60% of water depth up from the bottom), the data can be applied without the need for transformation. The cumulative burst performance curve in Figure 5.2 shows that relatively few of the fish tested were only able to achieve burst speeds at the lower end of the range, therefore the impact of this effect is not great.

5.3   Barbel

Barbel performed well in both burst and endurance tests, and consistently demonstrated the highest burst and endurance swimming speeds of all the species tested to date. This is perhaps not surprising, given their preference for swiftly flowing reaches of river, streamlined body shape, and large pectoral fins that are ideally suited to life in the flow.

In addition to their swimming ability and streamlined shape, barbel also appeared to be particularly good at finding any low velocity areas. In endurance swimming trials barbel tended to bunch together, often on the sides of the flume, or behind the group of fish in the section upstream. This "slipstreaming" meant that not all the fish were continually exposed to the full test velocities, and as the fish periodically shifted positions, it was not possible to determine which individuals had benefited from this behaviour. A short-term solution was to periodically disturb any fish exhibiting this behaviour, so that they were forced to swim in the water column. A longer-term solution was to test fewer fish at a time, and in one section only; the problem of slipstreaming was thereby much reduced.

Apart from slipstreaming, the behaviour of barbel in endurance swimming trials was generally consistent, and levels of performance varied in a predictable manner. In most cases the median and lower quartile endurance times were 200 minutes at the lower end of the velocity range, demonstrating that at least 75% of the fish tested had completed the trial. The threshold level at which median endurance consistently fell below 200 minutes increased with increasing temperature, and with increasing fish length. For example, median endurance times for small barbel first fell below 200 minutes in the velocity categories of 0.55-0.6, 0.65-0.7 & 0.75-0.8 m s^{-1} at temperatures of 5-10, 10-15 & 15-20°C respectively.

In burst tests small and medium barbel both occasionally demonstrated the "cheating" behaviour observed with brown trout in burst tests during Phase 1. This involves a fish maintaining station in the water flow without continually beating its tail. In the case of barbel, this tended to occur right in the angle of the high-speed tunnel. Although this behaviour was observed in a number of different fish, it was rarely maintained for long, and while it may have offered a brief respite, it is not considered that the behaviour will have greatly influenced the mean CBSS attained..
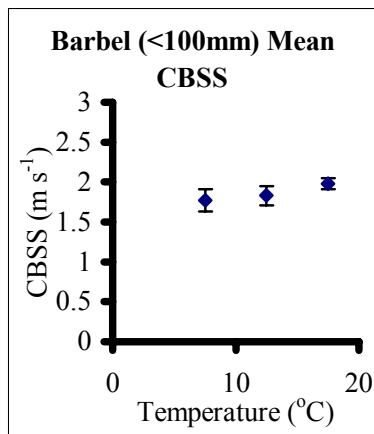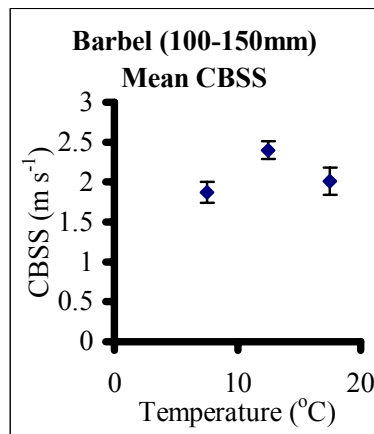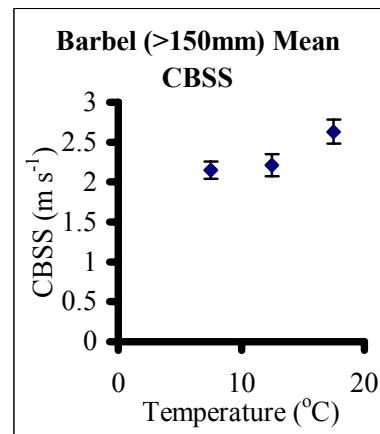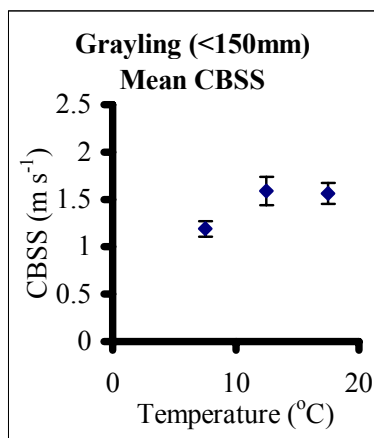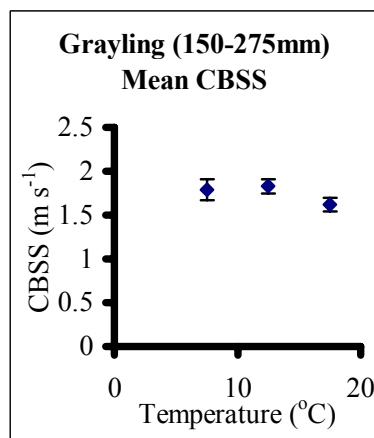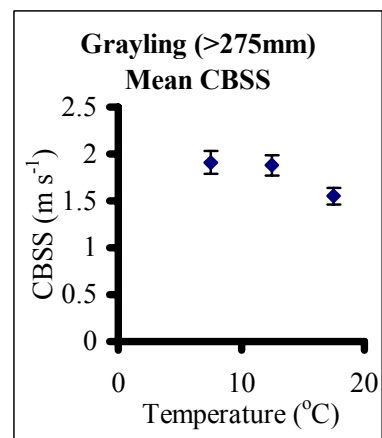
Figure 5.3a   **Figure 5.3b**   **Figure 5.3c**

Figures 5.3a, b & c. Mean critical burst swimming speeds of barbel in three size categories. Error bars are 95% confidence limits.

Burst swimming results for barbel are quite consistent across the size ranges, with most fish attaining burst speeds of between 1.5 and $2.5\,\mathrm{m\,s^{-1}}$. Mean CBSS increased with increasing temperature for small and large barbel (Figs 5.3a & c), but the highest mean CBSS values for medium barbel were found in the $10\text{-}15^{\mathrm{o}}$C temperature category (Fig. 5.3b). It is not clear why this should be the case, but it can also be seen in the equivalent chart with the water velocity given in body lengths per second (APPENDIX V, Fig. AV.1b), demonstrating that it was not an artefact generated by the growth of the fish within that length category.

The regression data show that for barbel, the relationships between CBSS and length (L)(P<0.001), and CBSS and temperature (T) (P<0.001) were both highly significant.

5.4   Grayling

From a fish husbandry point of view wild grayling were the most difficult of the species to work with to date. Fish were sourced from a number of rivers, and collected using a variety of techniques, however immediate post collection mortalities were consistently higher than seen in other species, particularly during the summer. In addition, fish collected from the wild invariably developed disease symptoms including reddened fins, raised scales and sore patches on the flanks. A number of treatments were tried, and some fish were sent away for analysis, but the causative agent was not identified, and a satisfactory solution was not found. It did however appear that water temperature and thermal stress played an important role in the development of symptoms as mortalities were significantly reduced once temperatures started to fall in the autumn. Hatchery - reared individuals were quite different and showed very low mortalities throughout the study period.

Grayling showed a generally reduced swimming performance in both endurance and burst swimming tests in the highest temperature category (Figs 5.4a-c). It is possible that this was an artefact generated by under-performance of fish that were not one-hundred-per-cent fit. Although fish that were obviously in poor condition were not used in tests, it is likely that some that appeared healthy were starting to deteriorate. Grayling are considered to be a "coldwater" species, and within the southern UK are approaching the southerly limit of their geographical range. It is likely that as they approach the upper end of their preferred

thermal range, swimming performance, or at least the motivation to achieve their maximum performance, is likely to fall. The fact that for small grayling endurance times were also reduced at the highest temperature, and burst performance was certainly not increased (Fig 5.4a), tends to point to the latter explanation, as the small, farmed grayling remained healthy throughout the study period.

Behaviour in endurance swimming trials was generally consistent, with the grayling continually swimming in the water column, just off the bottom of the flume. Periodically the fish would change position within the flume, and would occasionally drop downstream and contact the screen in the process; however unless they were displaying clear signs of fatigue, they were generally able to resume normal swimming. As fatigue increased, these positional shifts and collisions with the screen became more frequent, until the fish was unable to resume normal swimming. As a result, performance in endurance trials was quite variable.

Figure 5.4a   Figure 5.4b   Figure 5.4c
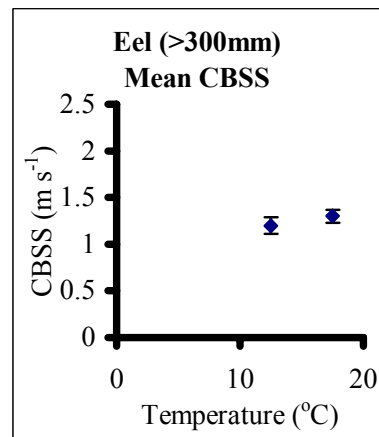
Figures 5.4a, b & c. Mean critical burst swimming speed of grayling in three size categories. Error bars are 95% confidence limits.

Mean CBSS of grayling tended to increase with increasing size, except in the highest temperature category where each size class tended to be around the 1.5 metres per second mark (Figs 5.4a-c).

The danger with using length categories, particularly with a species where a high turnover of individuals occurs, is that while one batch of fish may be centred around one end of the length category, the next batch, collected from a different source, or at a different time of year, could easily be centred at the opposite end of the length category. In the case of grayling, there was no significant difference in the mean lengths of the small and large fish in each of the temperature categories. The mean length of medium grayling tested at >15°C was, however, significantly lower than that of the same group tested in the two lower temperature categories (Figure 5.4d).
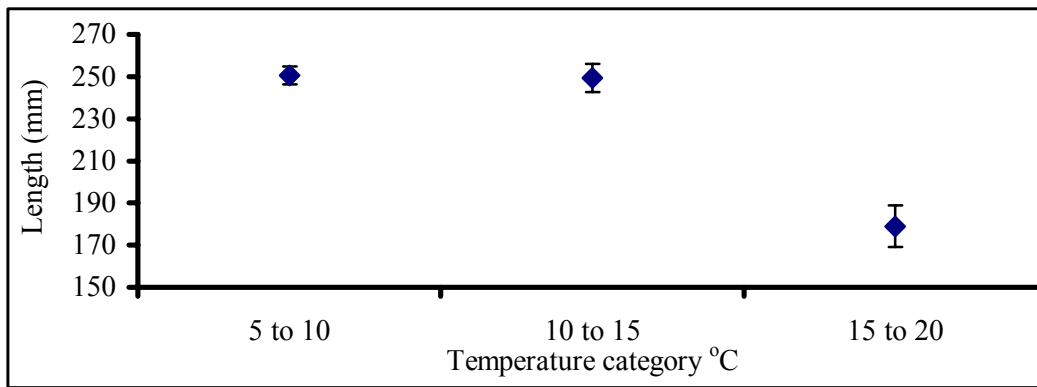
Figure 5.4d

Figure 5.4d. **Comparison of mean fish length of the 150-275mm length category of grayling, tested in three temperature categories. Error bars are 95% confidence limits.**

The reduction in mean CBSS seen in the medium grayling at the highest temperature category could, therefore, reflect the fact that these fish were on average smaller. Indeed, the equivalent chart, with the water velocity displayed in body lengths per second, shows a statistically significant rise in mean CBSS in the highest temperature category (APPENDIX V, Fig AV.2b). Whether this reflects a real improvement in swimming performance, or the predictable increase in the body lengths per second figure due to the reduced fish length, is not clear.

The regression data show that while there was a highly significant relationship between CBSS and length (L) (P<0.001) in grayling, the relationship between CBSS and temperature (T) was not significant (P=0.127).

5.5   Eel

The swimming performance of eels of all sizes was generally poor in comparison with the other species tested to date.

Eels in endurance trials frequently attempted to escape from the flume, suggesting that they were not entirely comfortable carrying out sustained swimming. Indeed, the propensity for eels to escape from the endurance flume necessitated the use of a specially constructed flume box, which had an open water surface, but was covered to prevent escapees. Because the high-speed tunnel is sealed eels were unable to escape, but overall performance was also generally poor.

Critical burst swimming speeds of eels were generally between 1 and 1.5 metres per second. The mean CBSS charts for eels are fairly consistent across the sizes, showing a slight, but non-significant rise with increasing temperature (Figs 5.5a-c).

Regression data for eels show a significant effect of length (L) on CBSS (P<0.001), however the relationship between CBSS and temperature (T) was not significant (P=0.01)
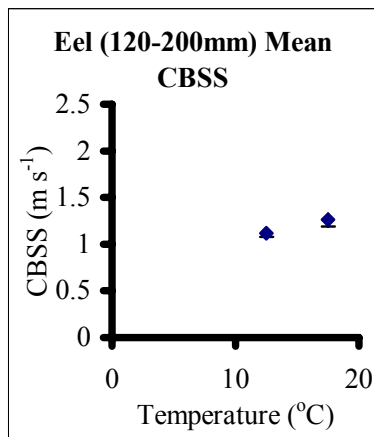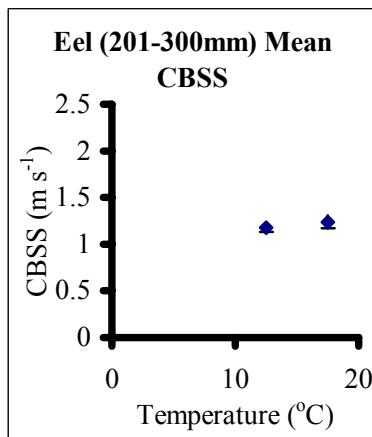
Figure 5.5a   Figure 5.5b   Figure 5.5c

Figures 5.5a, b & c. Mean critical burst swimming speeds of eels in three size categories. Error bars are 95% confidence limits.

5.6   Bream

Bream were generally weaker swimmers than barbel and grayling of equivalent size, and performed less well in burst and endurance trials. Nevertheless, the performance of bream in endurance trials showed a general increase with increasing temperature, and the level of performance is a direct reflection of their reduced swimming ability compared with the other species. This is consistent with the preference of bream for the slow flowing and sluggish reaches of rivers.

In burst tests at the coolest temperatures, using the standard CBSS methodology adopted for other species, it became apparent that a number of the fish tested failed to reach the first change of water speed at 20 seconds. This meant that the calculation of CBSS would not be representative, as it uses the last speed at which the full 20 seconds was achieved, and assumes a linear increase in water velocity between increments. To overcome this effect, the bream burst test methodology was adjusted to offer a slower start speed, to ensure that each fish had completed at least 20 seconds at a given speed, allowing a more realistic calculation of CBSS. The results, however, were quite unexpected and showed that, for the same group of fish, the slower start speed had resulted in a significant increase in the maximum CBSS attained of around 0.4m s^{-1}. In light of these findings a further, limited test was conducted, specifically to test the effect of start velocity on the CBSS of bream. In this trial, carried out in the highest temperature category, 15 fish were tested with start velocities of both 0.6 & 0.8m s^{-1}. Although the mean CBSS of the fish when started at 0.6 m s^{-1} was again slightly higher than when the same fish were started at 0.8m s^{-1}, the numbers tested were quite small, and the difference was not significant at the 95% level of confidence.

It was decided that further testing could shed more light on this issue and an additional 63 fish were then tested in the highest temperature category using the slower start speed, and a further 45 fish were tested in the 10-15°C category, with the faster start speed. This ensured that at least 45 fish had been tested with each start speed, in each temperature category (Figure 5.6). The results demonstrated that starting water velocity had no significant effect on the critical burst swimming speeds of bream at temperatures in excess of 10°C. Given the highly significant difference in performance in the 5-10°C category, it is not clear why this difference does not persist at higher temperatures. It is possible that the slower start speed provides the swimming muscles with an opportunity to "warm up",

and that once warmed up the fish are able to attain greater speeds, than when starting from cold. This would also account for the fact that no difference in burst speed was seen when the muscles were already warm, i.e. in the higher temperature categories. These additional tests, using the faster start speeds were not used in the SWIMIT v2 computer programme.

Only small bream were studied, and critical burst swimming speeds were generally between 1 and 1.5 metres per second. When comparing like with like, bream tested with the slower start speed showed a decreasing burst swimming capacity with increasing temperature (Figure 5.6). This is in complete contrast to the increased swimming performance seen in endurance trials, and is puzzling. Initially, it was considered possible that this was because the fish had grown, and that the reduced performance at the highest temperature was achieved with smaller fish. This pattern, however, remains evident when the data are plotted in body lengths per second, and is significant at the 95% level (APPENDIX V, Figure AV.4). Analysis of the length data shows that while there is no significant difference in fish length between the 5-10°C and 10-15°C temperature categories, the fish tested in the 15-20°C were in fact significantly larger than at the cooler temperatures. It is unlikely that the reduction in performance with increasing temperature corresponds to a reduction in ability, particularly as the same trend was not observed in the endurance trials. Instead it is more likely that the trend represents a reduced motivation to achieve their full capacity in burst trials, and may be linked to the seasonal distribution of water velocities in their natural habitat, namely the lower reaches of lowland rivers. In any case, it is further evidence that the swimming capacity of bream is strongly influenced by water temperature.
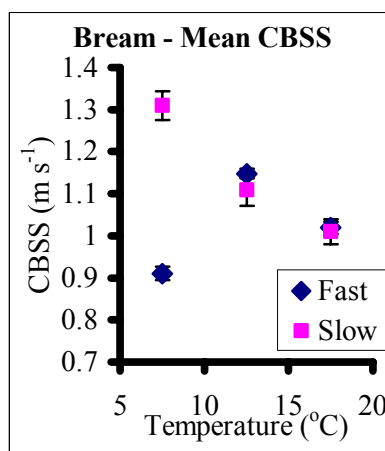
Figure 5.6

Figure 5.6. Mean critical burst swimming speeds of bream in three temperature categories, and at two different start velocities. Error bars are 95% confidence limits.

Only one size class of bream was tested, so it perhaps not surprising that within this length (L) category the relationship between length and CBSS was not significant (P=0.055). The relationship between temperature (T) and CBSS was, however, highly significant (P<0.001).

5.7   Burst Regression Analyses

Multiple regression analysis of CBSS on fish length and temperature (Tables 4.2a-d) showed that these factors accounted for a significant component (P<0.001) of the

variability in burst swimming performance, although each one to different degrees in the various species. The overall coefficients of variation (multiple-R^2), which ranged from 0.04 to 0.32, imply that the regressions account for only between 4% and 32% of the total variability. This reveals considerable variability in swimming performance due to factors not associated with length and temperature which, for the present, must be interpreted as 'random variability'. The 'random' component will, in reality, comprise the normal (in the statistical sense) variability of swimming ability within a population, as well as artefacts caused by the stresses of handling and confinement. This means that generous safety margins must be applied when referring to mean values. Within the SWIMIT programme, 90th percentile values are also given to take some account of this matter.

5.8 'SWIMIT' version 2.0

The computer programme SWIMIT has been extended in version 2.0 to include the species studies in Phase 2. The functionality of the programme is the same as for version 1.0. Within SWIMIT v2.0, burst speeds are calculated using the multiple regression data presented within this report, and endurance data are calculated from the endurance curves.

One additional species is included in SWIMIT version 2.0. Swimming speed tests on the European smelt, *Osmerus eperlanus*, were carried out under a separate project funded by Thames Water Utilities Ltd (TWU). Data for smelt have been included in SWIMIT v2.0 by kind courtesy of TWU. A synopsis of the smelt tests is included in APPENDIX VI.

5.9 Comparison of results with literature data

It is of interest to compare the results for the Phase 2 test species with the sparse data found in the literature for these or closely related species. 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 the related Arctic grayling (*T. arcticus*), he gives the coefficients as K = 36 and *e* = 0.19. Figure 5.7 compares the curve generated by Northcote's formula with values generated by SWIMIT v2.0. While Northcote does not give any indication of the water temperatures relating to his formula, it is clear that there is a good correspondence with SWIMIT v2.0 outputs generated for a selection of temperatures.

For the other species, the literature provides little help. Information for eels is restricted to data for elvers (covered in the Phase 1 study). The maximum sustained swimming speed of barbel is recorded as being 2.4 m s^{-1}, (Kreitmann, 1932 cited in Varley, 1967). This seems rather high compared with values of generally <1 m s^{-1} in this study but it is not clear how their figure was derived, nor how large they were (the maximum barbel size tested here was only 25cm). This author also gave a maximum sustained swimming speed for bream of 0.6m s^{-1} but with no other information on size or temperature.
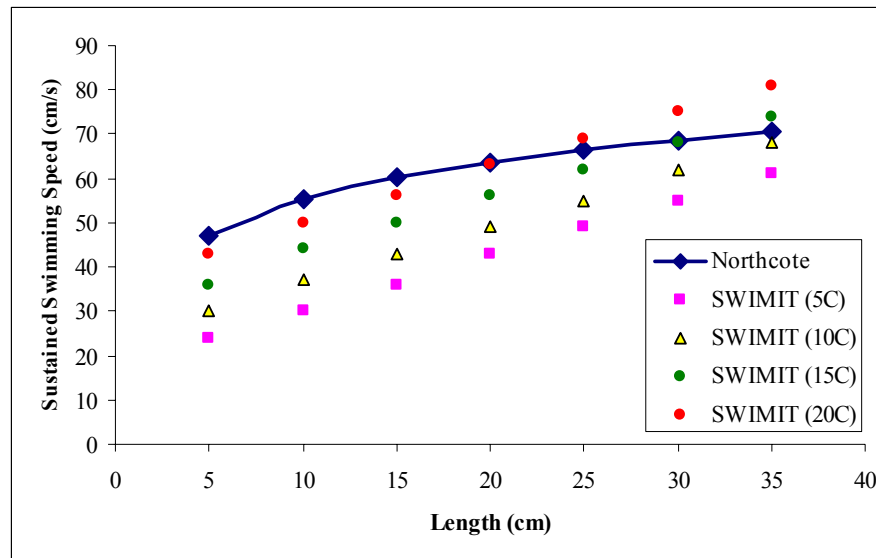
Figure 5.7 Comparison of data for *T. arcticus* generated by Northcote (1998) equation (temperature not stated) with values generated by SWIMIT v2.0 for *T. thymallus*.

5.10   Application of the data

5.10.1 Laboratory versus field conditions

The data presented here are based on controlled-environment laboratory conditions and provide a good indication of the capabilities of fish and of the likely spread of performance within a population. For reasons associated with fish keeping and handling, it can be expected that at least some fish may have been more stressed than might occur in the wild, perhaps accounting for the high degree of variability. To reflect the variability, data generated by the SWIMIT computer programme are given in terms of mean/median values, along with 90th percentiles. The latter provide a more precautionary option than the mean or median and perhaps overstate the true degree of spread that can be expected in the wild. The choice of which value to use is down to the individual user.

Other factors to consider when applying data to natural situations have been discussed elsewhere in this report and include:

- hydraulic conditions (bed roughness, turbulence) and
- motivational status of the fish.

Small-scale turbulence (relative to the length of the fish) within e.g. a baffled fish pass may not be an issue, as the velocities will tend to 'average' over the body of the fish, whereas large scale turbulence may disorientate the fish and not allow it to achieve its true performance. The key issue with bed roughness is that friction and small-scale turbulence near the bed will create a low-velocity boundary layer that smaller fish can exploit. This type of behaviour was observed regularly in our experiments using 0-group fish, where surfaces were invariably smooth (stainless steel or GRP); on stony substrates this effect will be exaggerated and, consequently, larger fish will be able to take advantage of the boundary layer. In general, therefore, fish in the wild can be expected to perform better in

upstream migration against a flow than laboratory results would indicate. Again, therefore, the results of this study will lead the user to err on the side of caution. Of course, it may be possible to quantify the boundary condition and eliminate this source of error in some applications.

Motivational status is particularly difficult to account for. Many previous studies of fish swimming have used electric shocker systems or other forms of goad to 'encourage' fish to swim to their maximum capacity. Prior to the testing in Phase 1 of this project, the Project Board took a decision that strong artificial stimuli would not be used, so that the results would better reflect the conditions for which the data were intended to apply: after all, a fish ascending a fish pass will not generally be being chased. It is acknowledged, though, that under certain conditions in the wild, fish may be more strongly motivated to swim than in our tests. This is a further example of how application of the experimental data might provide a safety margin relative to the wild situation.

5.10.2 Application to design of water intakes

A number of sources provide guideline criteria for setting maximum permissible water velocities at water intakes to reduce the risk of fish entrainment or impingement, for example, the Salmon Advisory Committee give criteria for salmonids, while Solomon (1992) and Turnpenny *et al*. (1998) cover salmonids and coarse fish. These are 'broad-brush' criteria, as opposed to ones that may be tailored to the particular sizes of fish that occur in a specific location, or that take account of the season and water temperatures when non-resident fish may come into contact with the intake. SWIMIT may be used to make a more detailed assessment for specific cases where these factors are known. It can also be used when undertaking a risk assessment for a given intake design and location.

Several practical points should be borne in mind. Turnpenny *et al*. (1998) draw attention to the fact that intake velocity data presented by developers is commonly calculated simply as intake flow divided by the wetted intake cross-sectional area. In reality, distribution of flow across the intake opening is never uniform, owing to bed and wall friction and, especially in lateral intakes, due to momentum, which biases flow towards the downstream end of the intake. Therefore, it is the maximum velocity that should be estimated. This can be achieved through computational fluid dynamics (CFD) models or by measurement. Turnpenny *et al*. (1998) proposed using the maximum sustainable speed, taking the median population value and reducing it by one third to give a safety margin. Alternatively, the 90th percentile could be used, without the one-third safety margin.

It is not recommended that burst swimming speed data be used in setting intake design-velocities, as fish will normally respond with burst swimming only when startled. Possible exceptions to this are barriers where electric or acoustic stimuli are used.

5.10.3 Application to fish passes

Owing to the many different types of fish pass (pool-and-traverse, Denil, Larinier, vertical slot, etc.) now available and to the variants on the basic designs, more specialist texts should be consulted to learn more about the general design criteria and velocity conditions associated with different designs. Beach (1984) and Larinier *et al*. (2002) provide good starting points and draw attention to the main issues related to velocity, which may be summarised as follows:

- For pool-and-traverse and vertical-slot fishways, which involve ascent by stages, burst swimming speeds should be used; however, they should not be used in consideration of baffled pass designs where passage time is likely to exceed 20s.

- When considering baffled fishways, maximum sustainable speeds should be considered, along with the maximum endurance time estimated for a given velocity. This will determine the length of individual flights of the pass ascendable by fish of a given size and species at a given temperature.

- With regard to the scale-of-turbulence issue mentioned in s.5.10.1, bear in mind that it may not be an issue for a fully grown salmon or sea trout ascending a Denil pass, whereas the scale of turbulence may be large relative to a cyprinid, such as a roach, which becomes reproductively mature at a very much smaller size. Larinier *et al*. recommend that a safety margin is factored in to the design to allow for this. As indicated above, various margins of safety are implicit in the outputs from SWIMIT v.2, although small fish may not be able to ascend passes with large baffles which consequently lead to large-scale turbulence. Passes with smaller baffles, such as the Larinier design are helpful to small fish in this respect.

- The temperature considered in the designed should be that at which the poorest swimming performance is predicted to occur (in the UK, this will generally be the lowest temperature at which fish would migrate).

SWIMIT v. 2.0 will allow all the necessary swimming performance data to be estimated.

6.   CONCLUSIONS & RECOMMENDATIONS

1. A large number of fish were tested in both burst and endurance trials, and substantial data sets were generated.

2. There was a high degree of individual variation in fish performance both within and between tests.

3. Barbel consistently exhibited superior swimming performance to any of the other species tested in Phase 2.

4. Wild grayling were particularly difficult to keep in captivity, especially during the summer. The same problem was not encountered with hatchery reared individuals.

5. The swimming performance of grayling shows a general decline at high water temperatures, in both burst and endurance tests.

6. Eels are generally poor swimmers and performed less well in swimming trials than the other species tested to date.

7. It appears that for small bream, at the coldest temperatures, the start velocity can influence performance in burst swimming trials, but this does not appear to be the case at the highest temperatures. It is possible that at low temperatures the swimming muscles need time to "warm up" in order for fish to achieve their maximum burst swimming potential. If this is the case, it could have important implications for the wintertime operation of river management structures such as hatches and locks, as well as for future swimming speed trials.

8. The performance of bream in endurance swimming trials shows a general increase with increasing water temperature. This is in direct contrast to the significant reduction in CBSS with increasing temperature.

9. Literature data regarding the swimming ability of other native riverine species including pike, perch and larger bream are sparse and further testing with these species is justified.

10. Minor riverine species such as ruffe, bullhead, bleak and stone loach have generally not been considered in studies of swimming performance, and may warrant further investigation.

11. The computer program SWIMIT v.2.0 may be used to estimate swimming speeds of the average or median fish of a given size at a given water temperature, and also the 90%ile value. The latter helps to take account of the spread of performance within the population.

12. The experimental data generated here under laboratory conditions may include some fish that performed less well than they would in the wild, for reasons of handling and confinement. Also, they were tested in smooth channels with minimal boundary layer, unlike in many field situations where gravel or rocky substrates occur. The data therefore probably underestimate true performance in natural channels, thereby giving a margin of safety.

13. Provided that the hydraulics of the structure are properly taken into account, the data provided here, accessible via the SWIMIT v.2.0 computer program, provide a good way of factoring fish swimming performance into design of engineered structures such as water intakes and fish passes.

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APPENDICES

APPENDIX I. Sources of test fish.

Table AI. Details of fish used in swimming speed trials including source, numbers and date collected.

Species	Type	Origin	Number	Date
Barbel	Farmed	EA hatchery, Calverton	20	28/11/02
Barbel	Farmed	Hampshire Carp Hatcheries	50	19/11/02
Barbel	Farmed	Hampshire Carp Hatcheries	120	4/4/01
Barbel	Farmed	Hampshire Carp Hatcheries	120	4/4/01
Barbel	Farmed	EA hatchery, Calverton	197	30/3/01
Barbel	Farmed	EA hatchery, Calverton	150	30/3/01
Barbel	Farmed	EA hatchery, Calverton	30	18/4/02
Bream	Farmed	EA hatchery, Calverton	75	30/3/01
Bream	Farmed	EA hatchery, Calverton	75	30/3/01
Bream	Farmed	Moore & Moore Carp	100	9/7/01
Eel	Wild	River Itchen	1	30/3/01
Eel	Wild	River Adur	5	27/6/01
Eel	Wild	River Adur	9	27/6/01
Eel	Wild	River Thames	12	9/7/01
Eel	Wild	River Severn catchment	70	13/8/01
Eel	Wild	River Taff	50	31/7/01
Eel	Wild	River Meon	40	16/8/01
Eel	Wild	River Severn catchment	235	12/4/02
Eel	Wild	River Thames	35	11/9/02
Grayling	Wild	River Avon	90	6/10/01
Grayling	Wild	River Test	146	7/11/01
Grayling	Wild	River Avon	40	5/10/02
Grayling	Wild	River Wylye	51	11/3/02
Grayling	Wild	River Wylye	35	11/7/02
Grayling	Wild	River Test	85	19/2/02
Grayling	Wild	River Itchen	95	26/3/01
Grayling	Wild	River Test	100	31/7/01
Grayling	Farmed	EA hatchery, Calverton	70	30/8/01

APPENDIX II. Median endurance swimming charts with velocity data presented in body lengths per second.
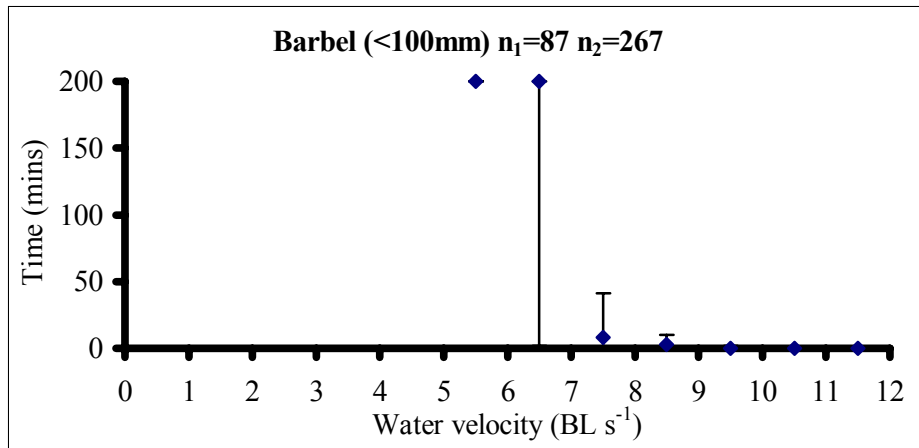
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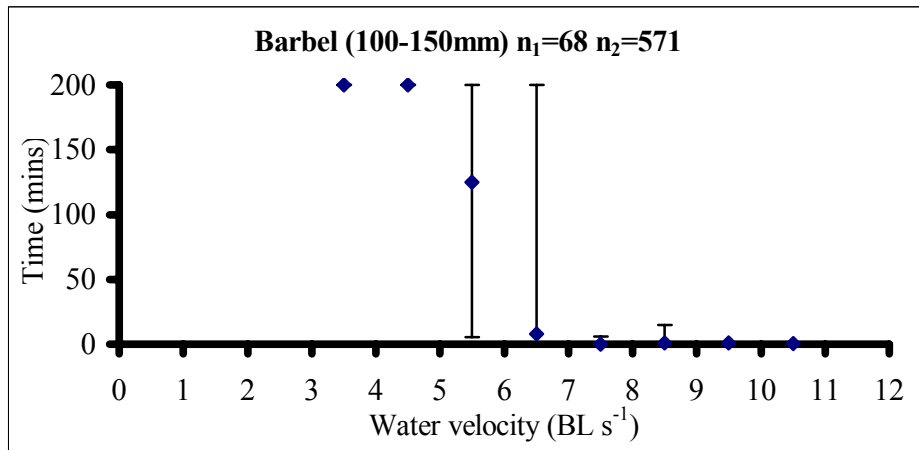
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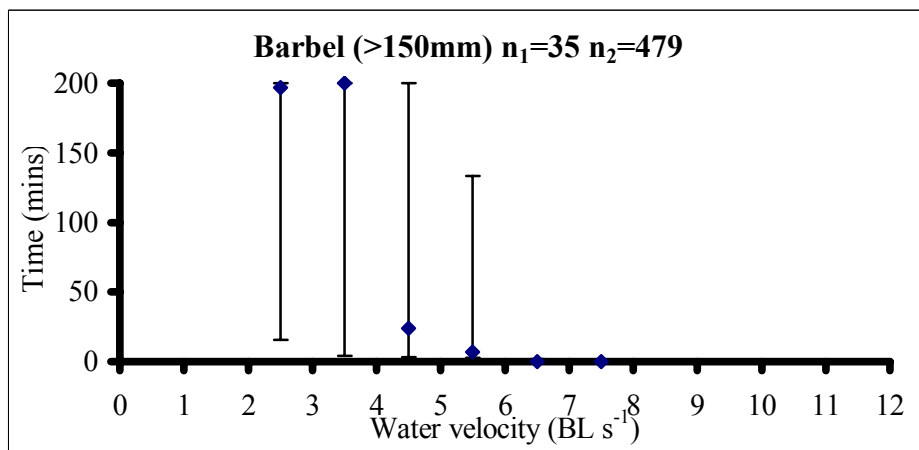
Figure AII.1c.

Figures AII.1a-c. Median endurance swimming speeds of barbel at 5-10°C. Error bars are upper and lower quartiles.
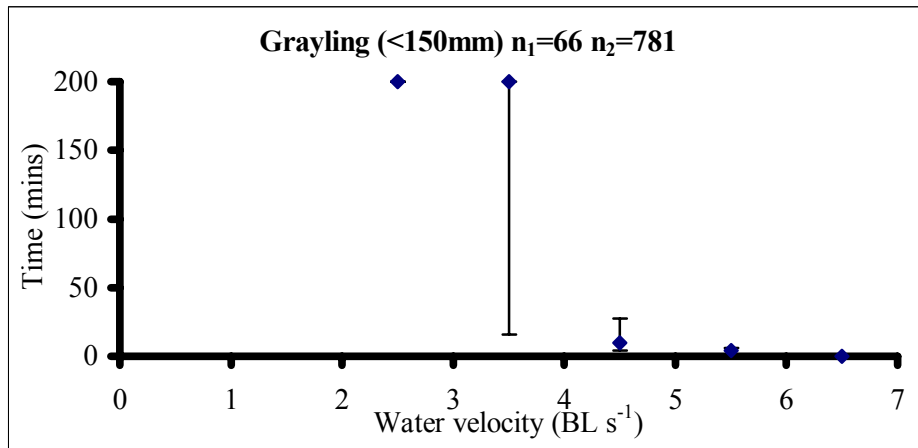
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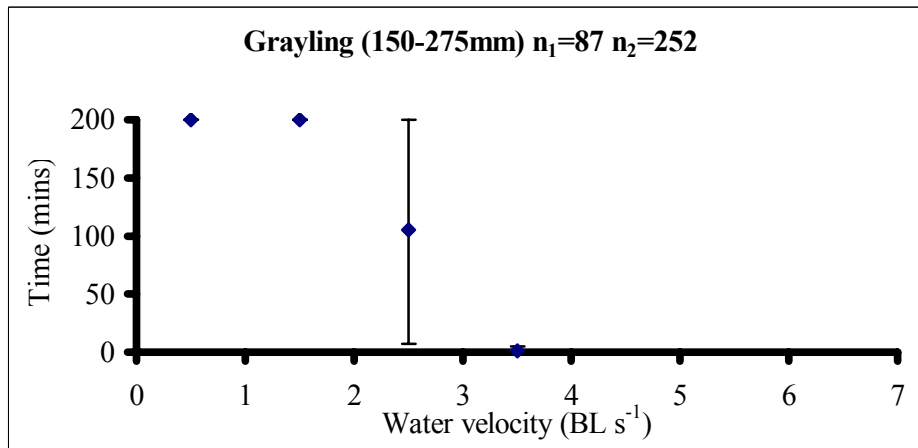
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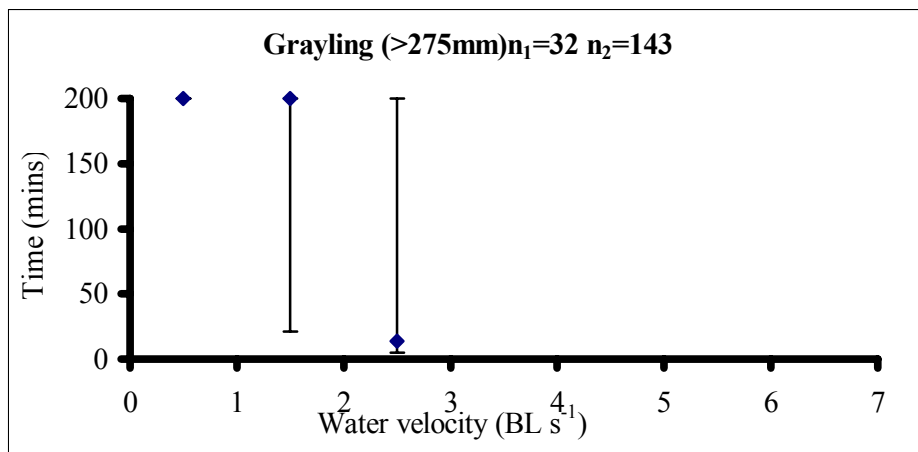
Figure AII.1f.

Figures AII.1d-f. Median endurance swimming speeds of grayling at 5-10°C. Error bars are upper and lower quartiles.
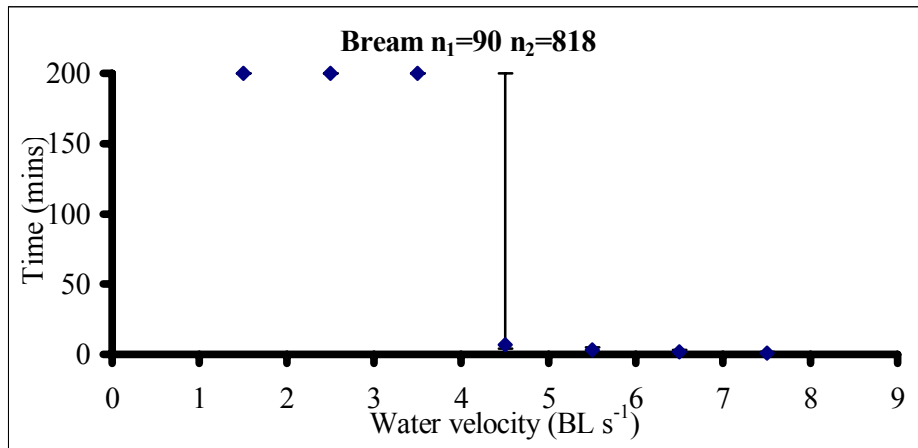
Figure AII.1g.

Figure AII.1g. Median endurance swimming speeds of bream at 5-10°C. Error bars are upper and lower quartiles.
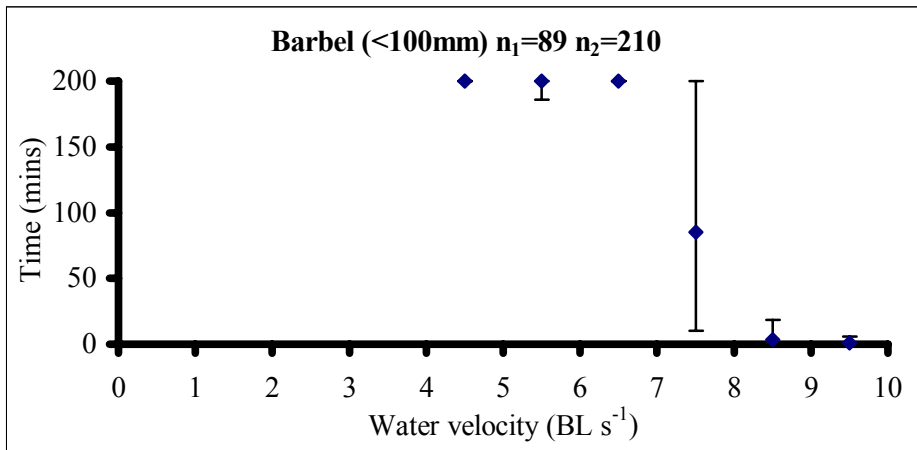
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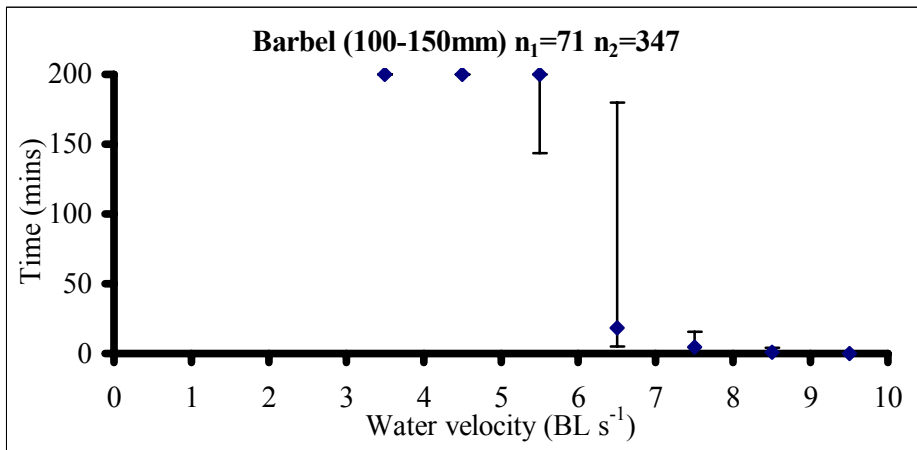
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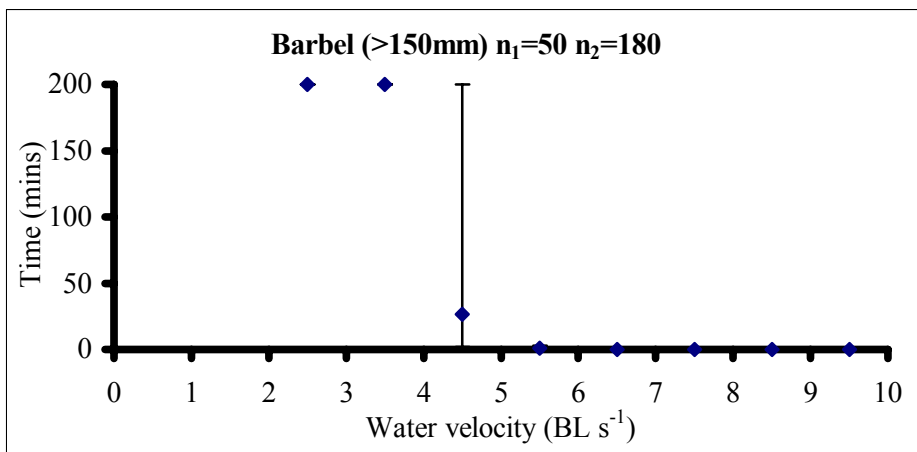
Figure AII.2c.

Figures AII.2a-c. Median endurance swimming speeds of barbel at 10-15°C. Error bars are upper and lower quartiles.
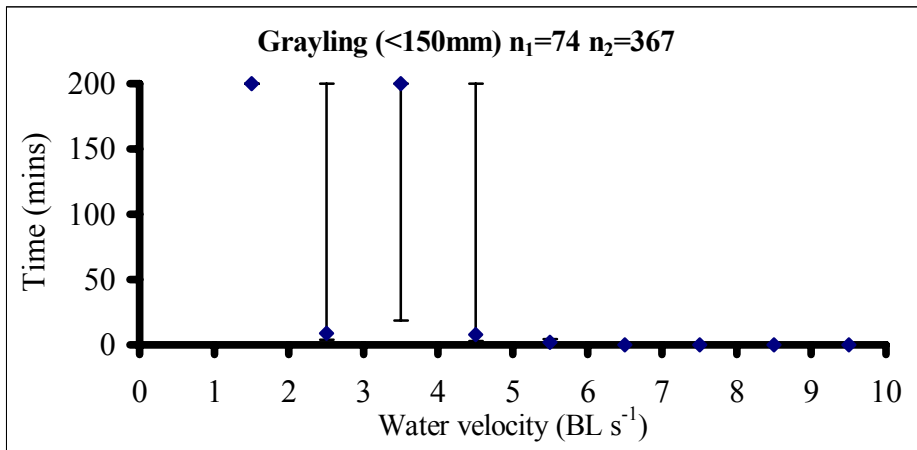
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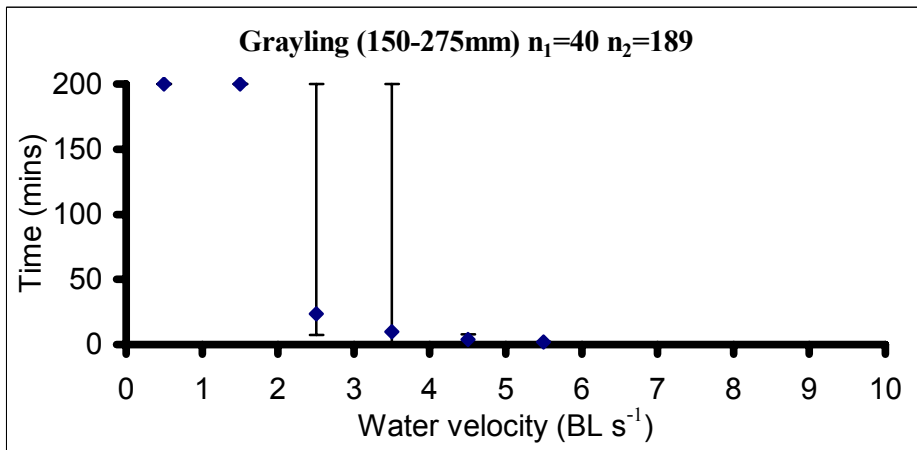
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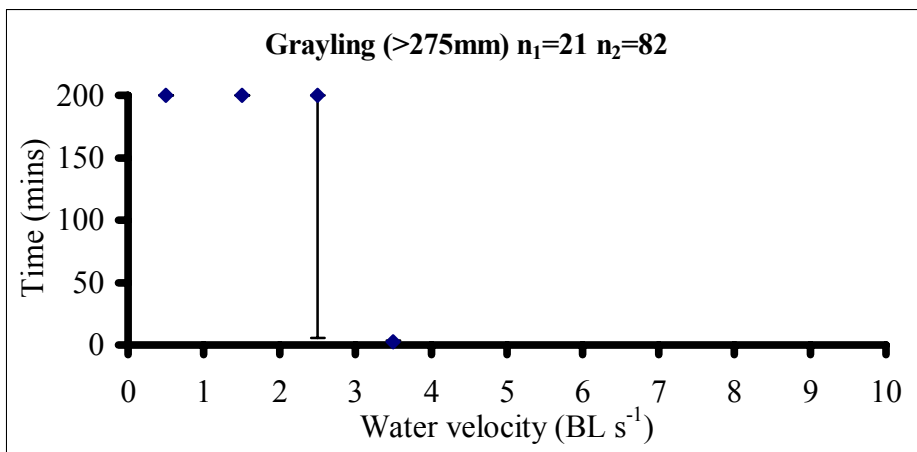
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Figures AII.2d-f. Median endurance swimming speeds of grayling at 10-15°C. Error bars are upper and lower quartiles.
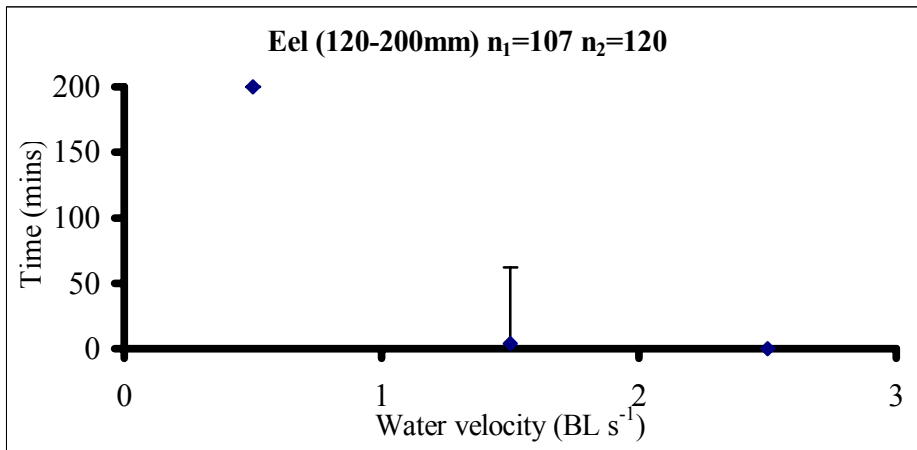
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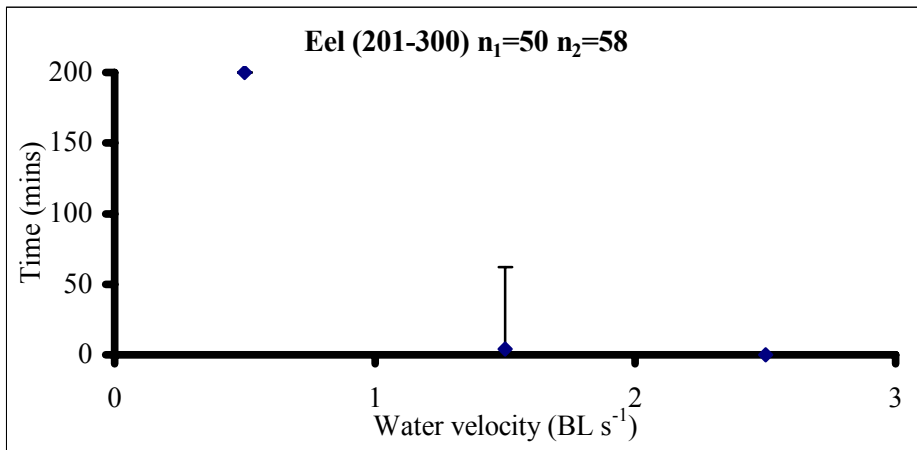
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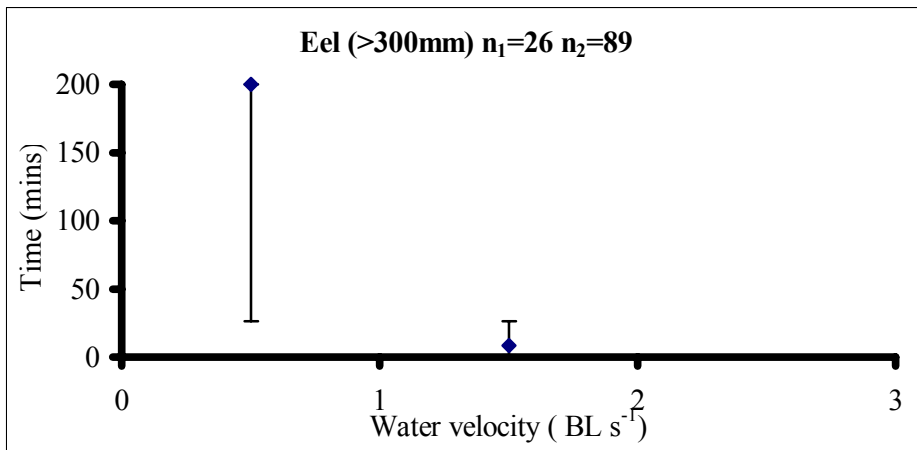
Figure AII.2i.

Figures AII.2g-i. Median endurance swimming speeds of eels at 10-15°C. Error bars are upper and lower quartiles.
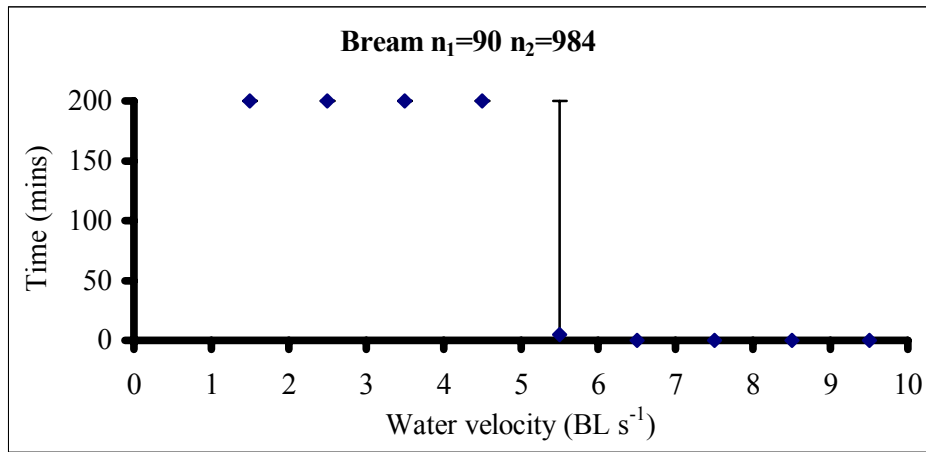
Figure AII.2j.

Figure AII.2j. Median endurance swimming speeds of bream at 10-15°C. Error bars are upper and lower quartiles.
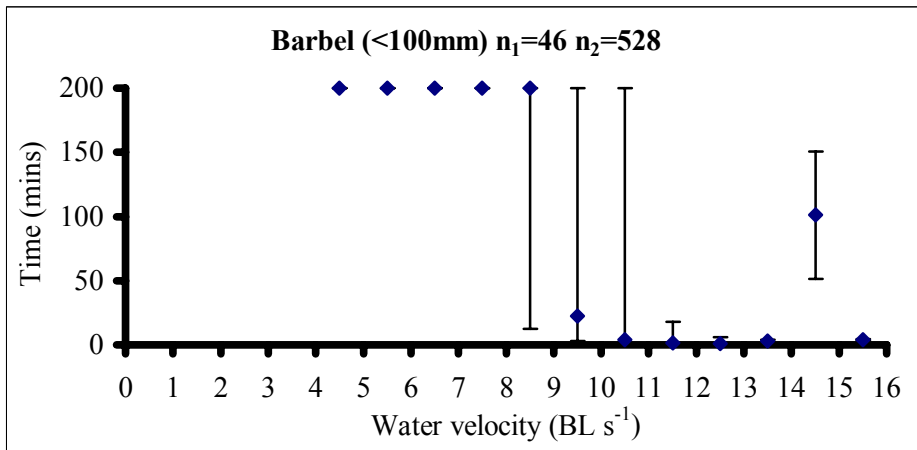
Figure AII.3a.
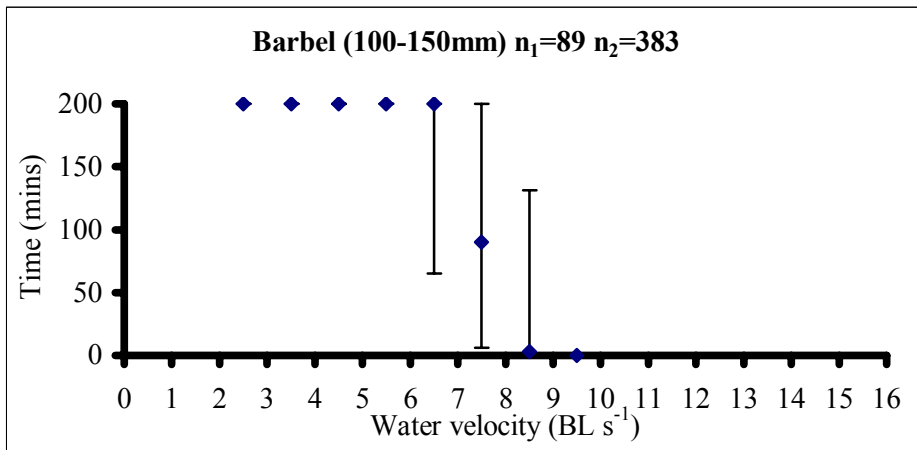
Figure AII.3b.
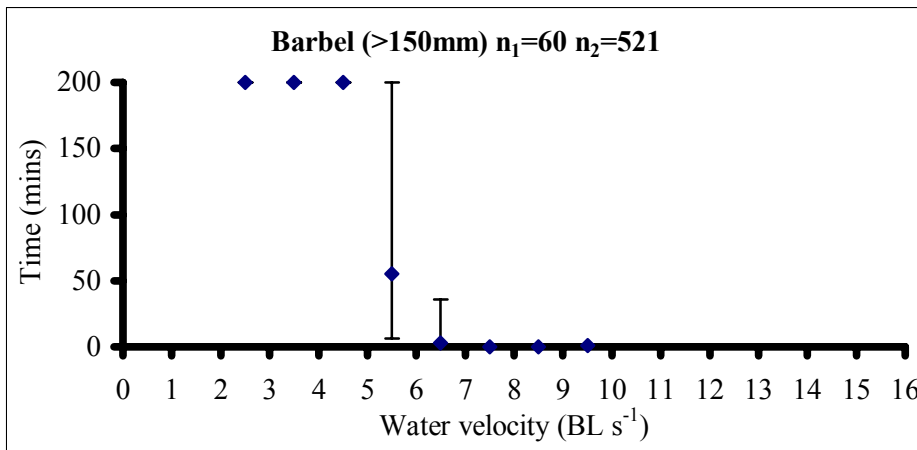
Figure AII.3c.

Figures AII.3a-c. Median endurance swimming speeds of barbel at 15-20°C. Error bars are upper and lower quartiles.
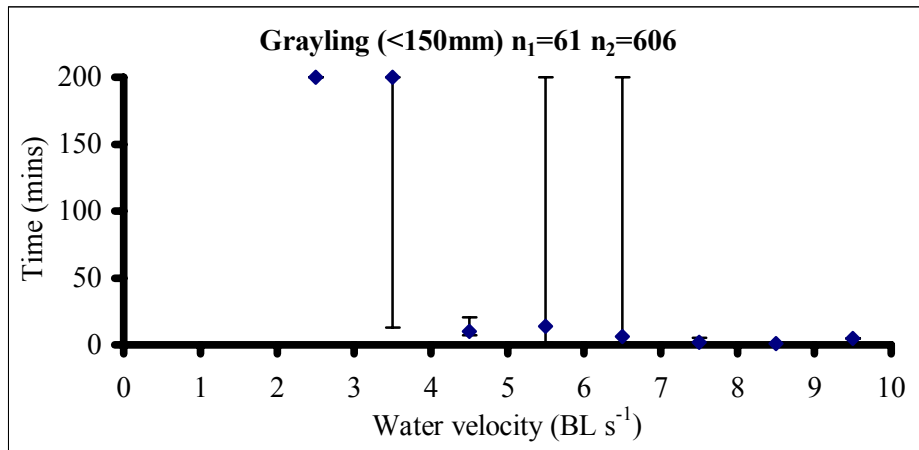
Figure AII.3d.
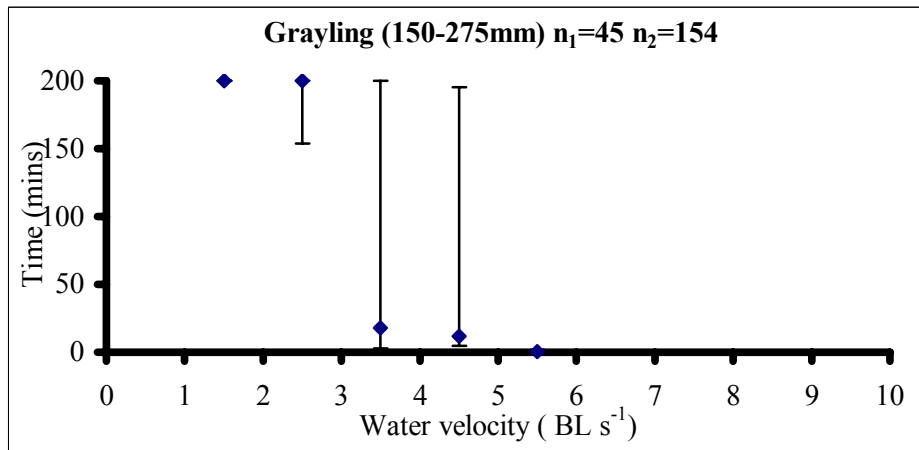
Figure AII.3e.
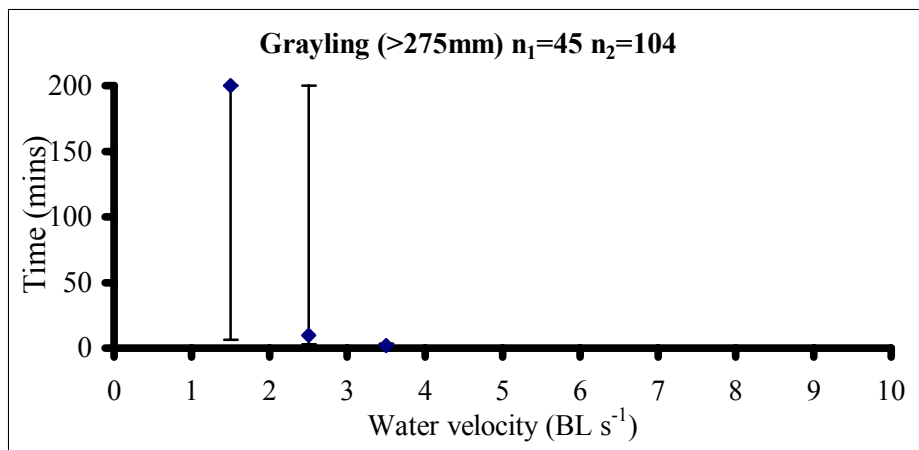
Figure AII.3f.

Figures AII.3d-f. Median endurance swimming speeds of grayling at 15-20°C. Error bars are upper and lower quartiles.
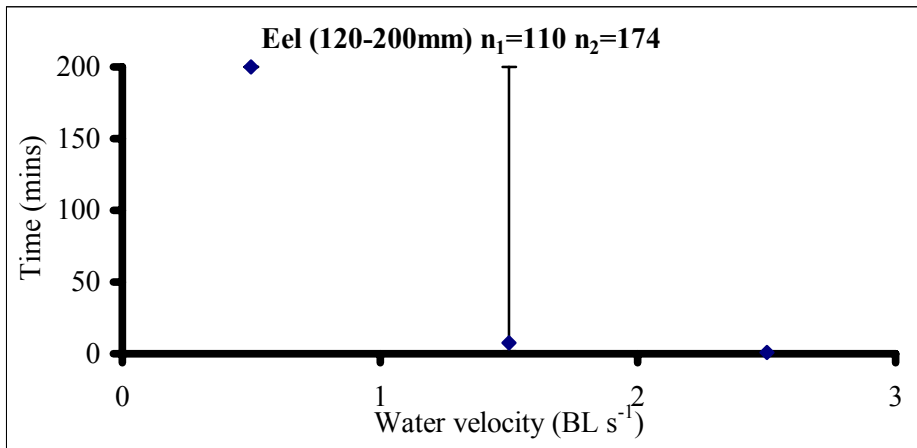
Figure AII.3g.
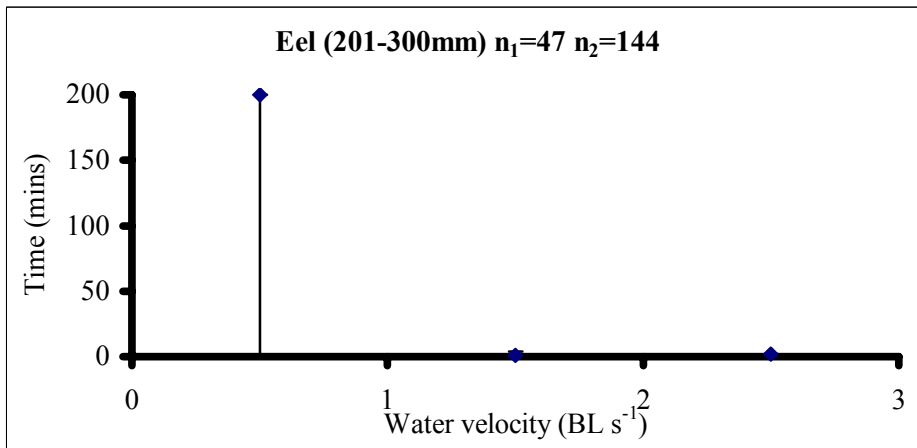
Figure AII.3h.
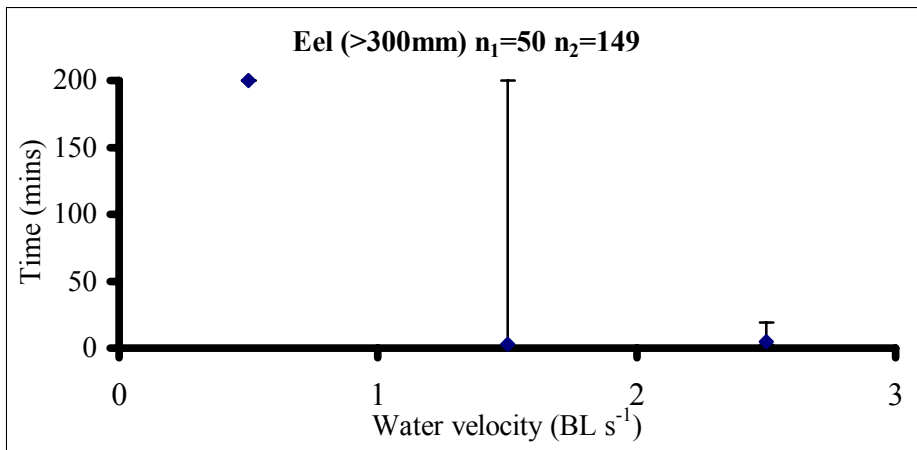
Figure AII.3i.

Figures AII.3g-i. Median endurance swimming speeds of eels at 15-20°C. Error bars are upper and lower quartiles.
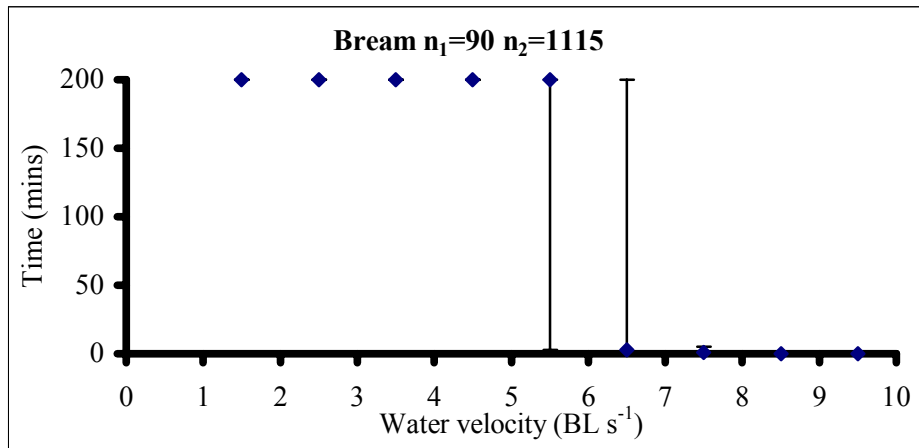
Figure AII.3j.

Figure AII.3j. Median endurance swimming speeds of bream at 15-20°C. Error bars are upper and lower quartiles.

APPENDIX III. Critical Burst Swimming Speed charts (data presented in metres per second).

AIII.2.1 Burst results 5-10°C
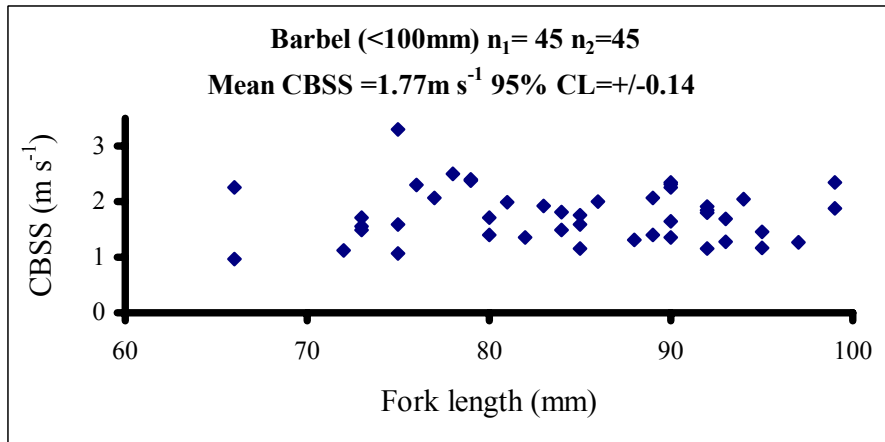
Figure 4.2.1a
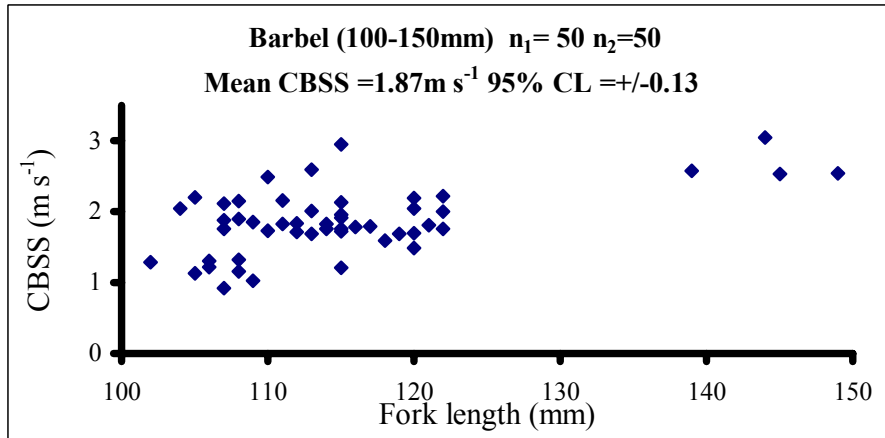
Figure 4.2.1b
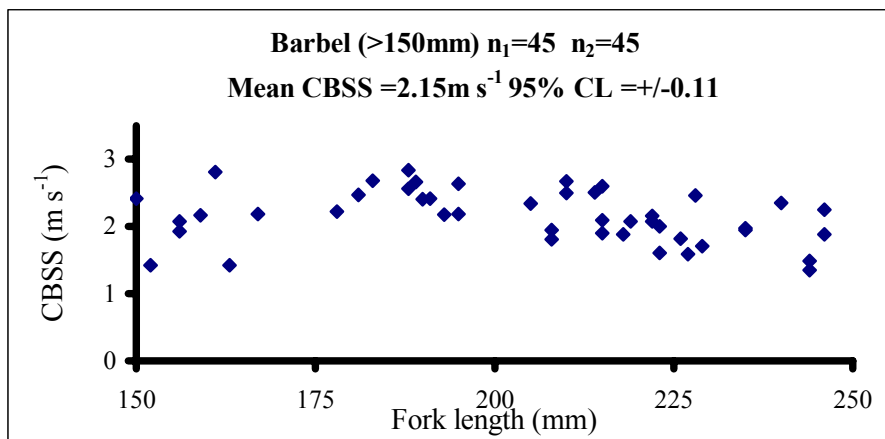
Figure 4.2.1c

Figures 4.2.1 a-c. Critical Burst Swimming Speeds of barbel at 5-10°C.
n_1 = no. of individual fish tested, n_2 = total no. of fish tested
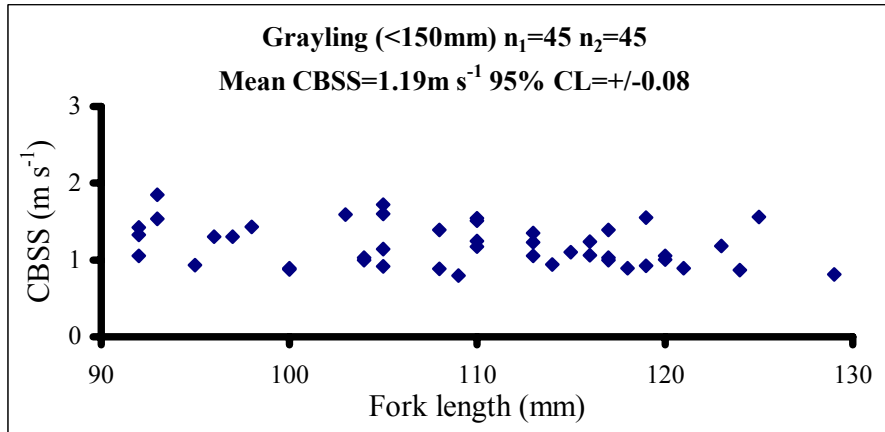
Figure 4.2.1d
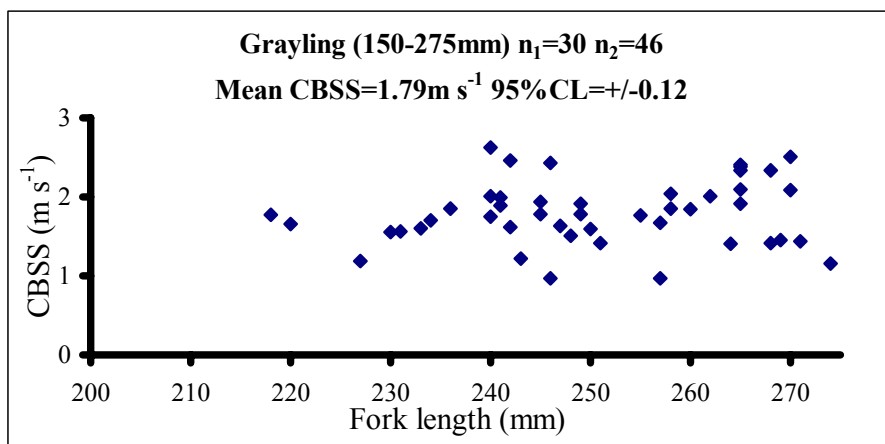
Figure 4.2.1e
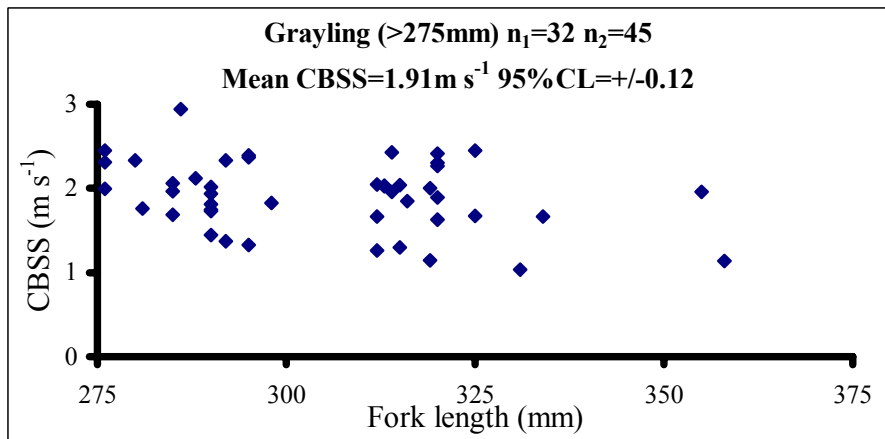
Figure 4.2.1f

Figures 4.2.1 d-f. Critical Burst Swimming Speeds of grayling at 5-10°C.
n_1 = no. of individual fish tested, n_2 = total no. of fish tested
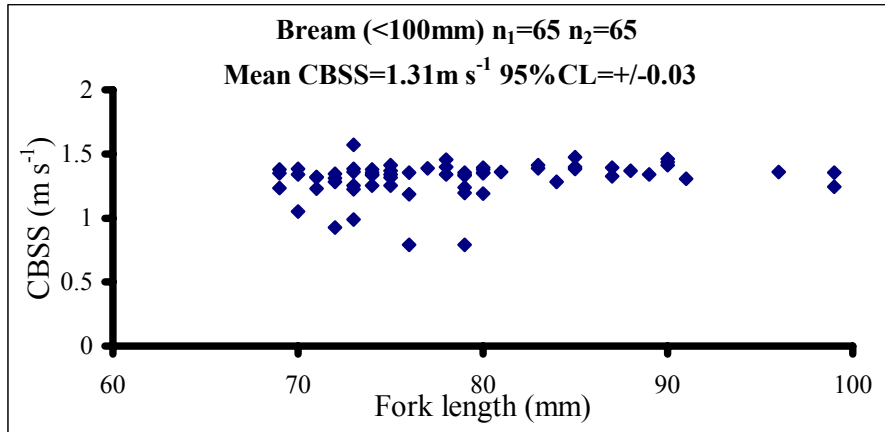
Figure 4.2.1g. Critical Burst Swimming Speeds of bream at 5-10°C.
n_1 = no. of individual fish tested, n_2 = total no. of fish tested

A4.2.2 Burst results 10-15 ^{o}C

Barbel (<100mm) n_1=86 n_2=48
Mean CBSS=1.83m s^{-1} 95%CL=+/-0.12

Figure 4.2.2a

Barbel (100 - 150mm) n_1=67 n_2=113
Mean CBSS=2.40m s^{-1} 95%CL=+/-0.11

Figure 4.2.2b

Barbel (>150mm) n_1 =35 n_2 =49
Mean CBSS=2.21m s^{-1} 95%CL=+/-0.14
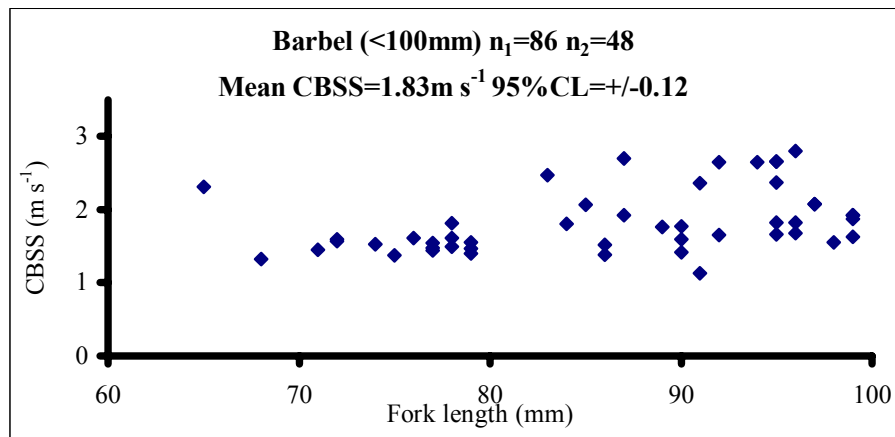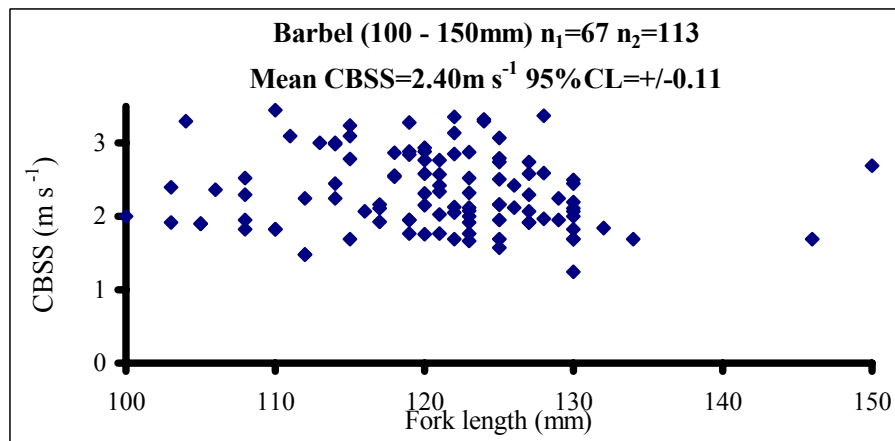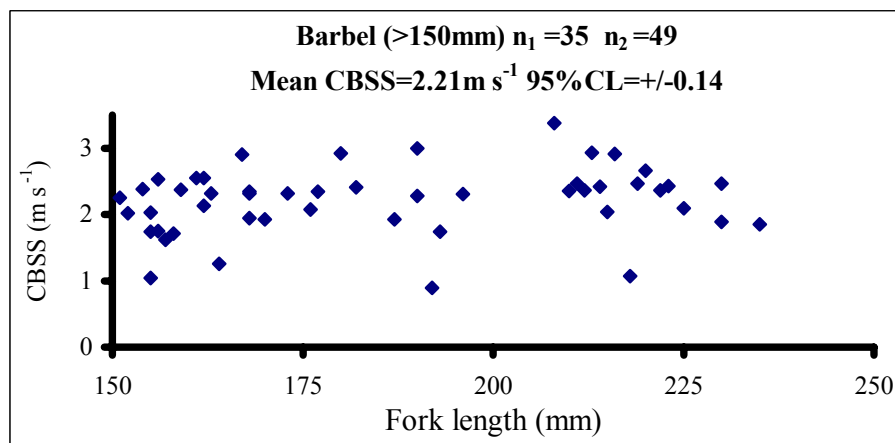
Figure 4.2.2c

Figures 4.2.2 a-c. Critical Burst Swimming Speeds of barbel at 10-15°C.
n_1 = no. of individual fish tested, n_2 = total no. of fish tested
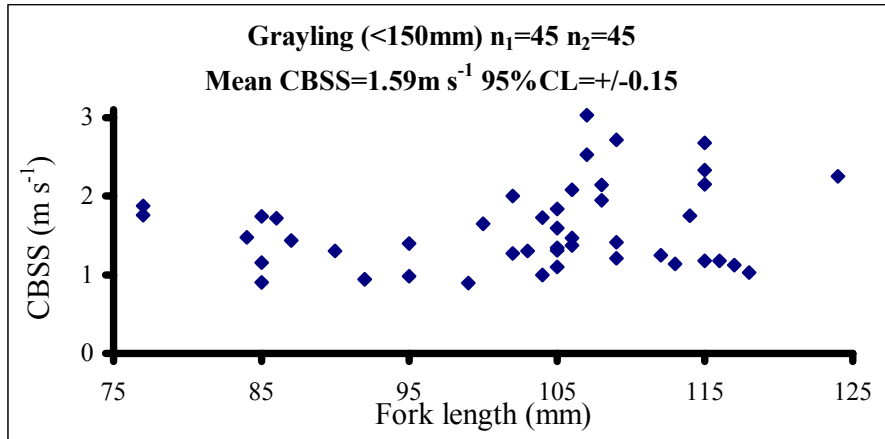
Figure 4.2.2d
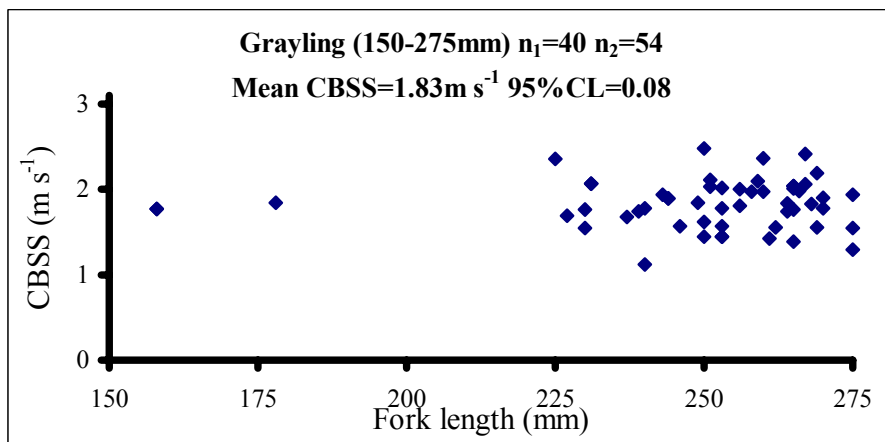
Figure 4.2.2e
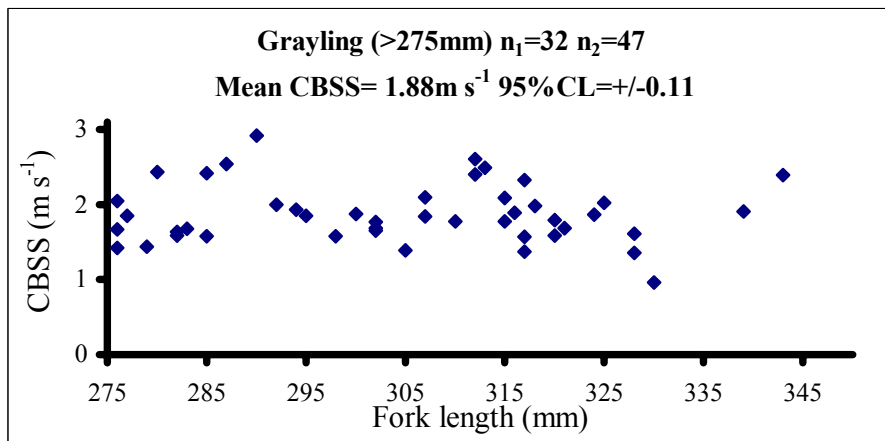
Figure 4.2.2f

Figures 4.2.2 d-f. Critical Burst Swimming Speeds of grayling at 10-15°C.
n_1 = no. of individual fish tested, n_2 = total no. of fish tested
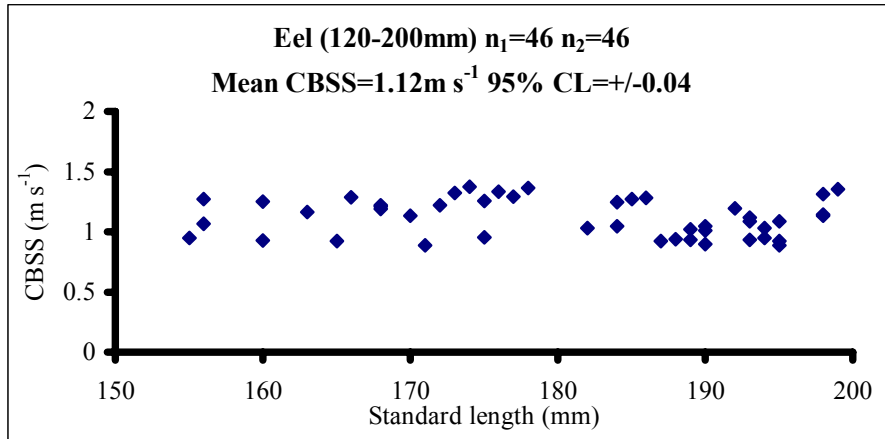
Figure 4.2.2g
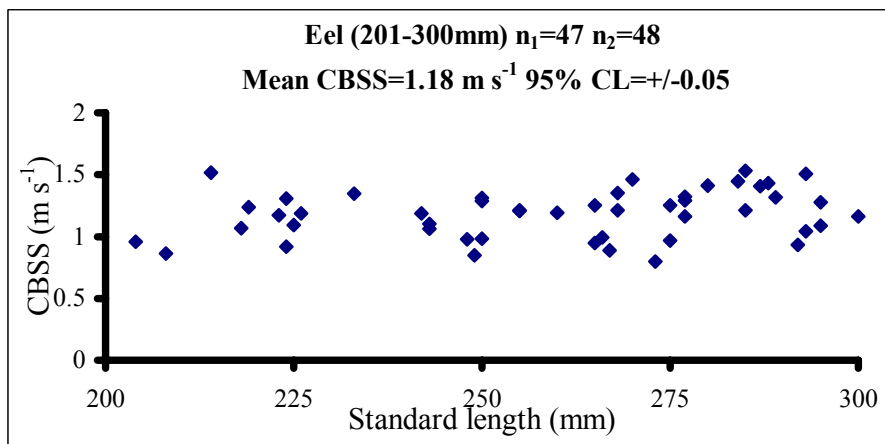
Figure 4.2.2h
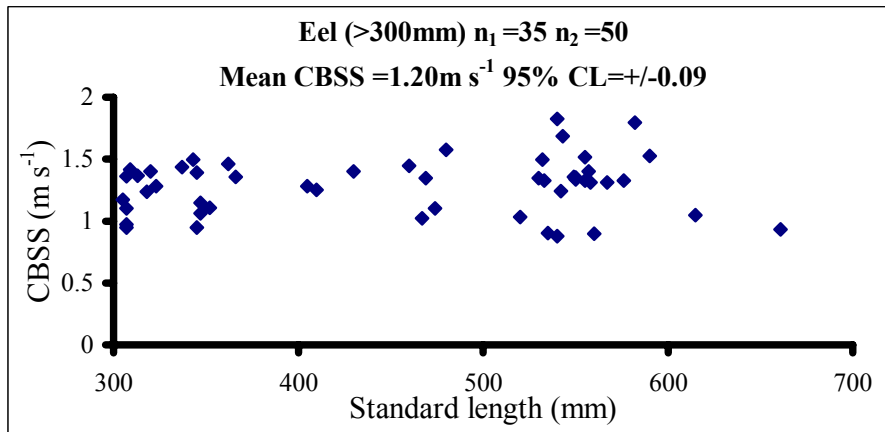
Figure 4.2.2i

Figure 4.2.2 g-i. Critical Burst Swimming Speeds of eels at 10-15°C.
n_1 = no. of individual fish tested, n_2 = total no. of fish tested
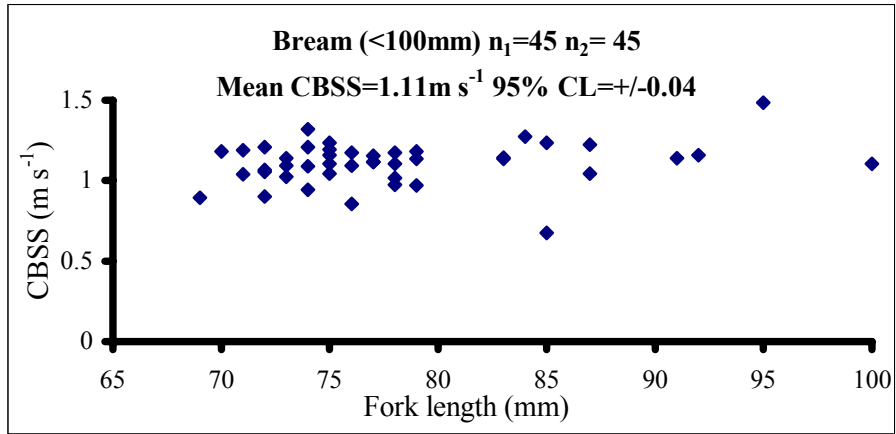
Figure 4.2.2j. Critical Burst Swimming Speeds of bream at 10-15°C.
n_1 = no. of individual fish tested, n_2 = total no. of fish tested

A4.2.3 Burst results >15 °C
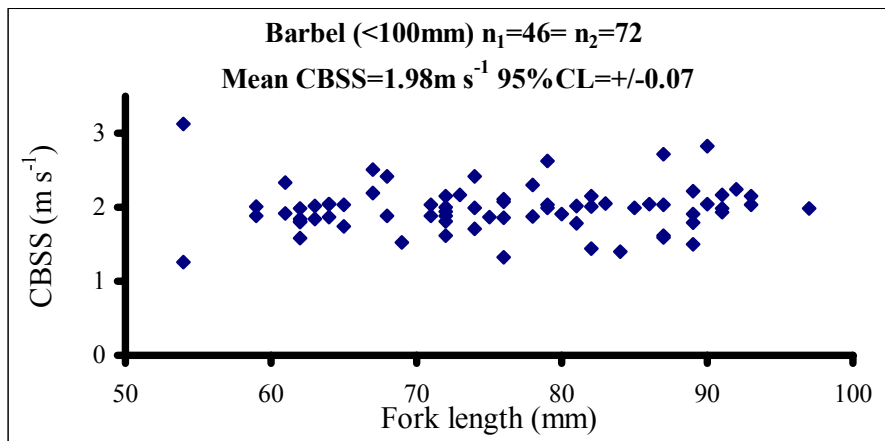
Figure 4.2.3a
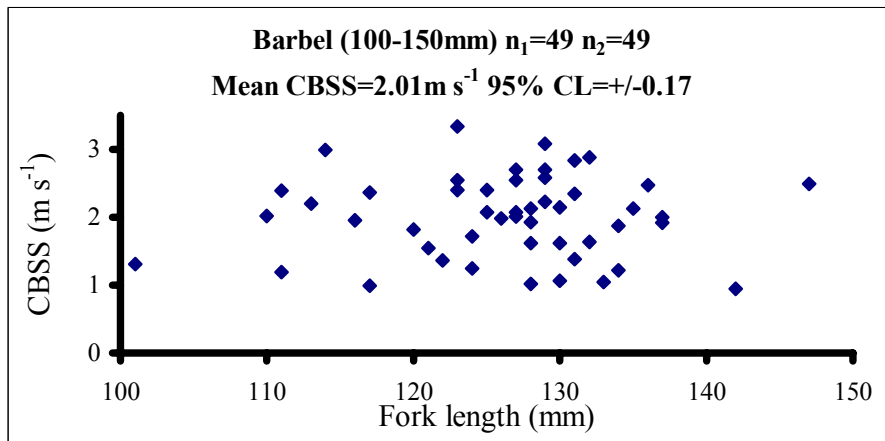
Figure 4.2.3b
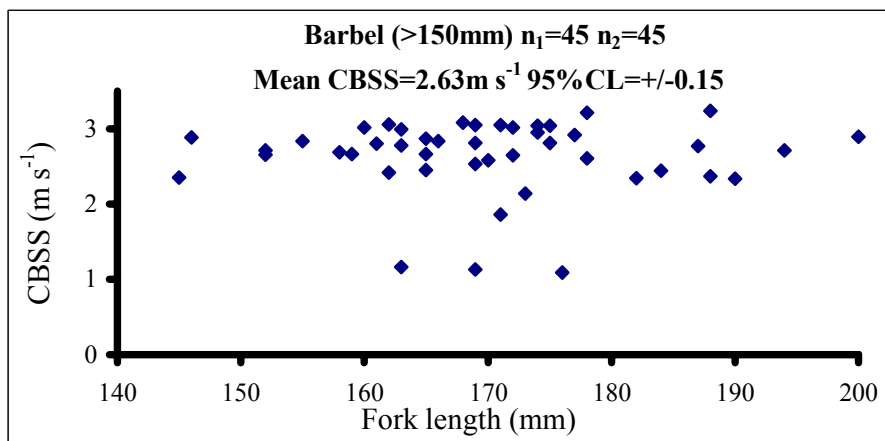
Figure 4.2.3c

Figures 4.2.3 a-c. Critical Burst Swimming Speeds of barbel at >15°C.
n_1 = no. of individual fish tested, n_2 = total no. of fish tested
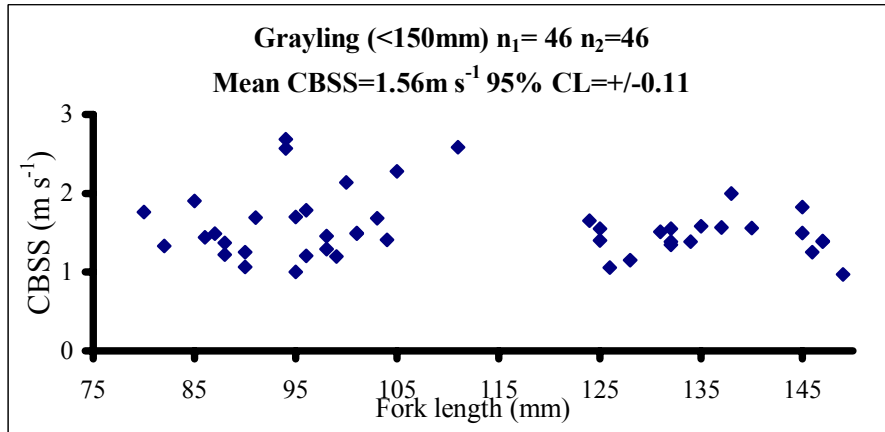
Figure 4.2.3d
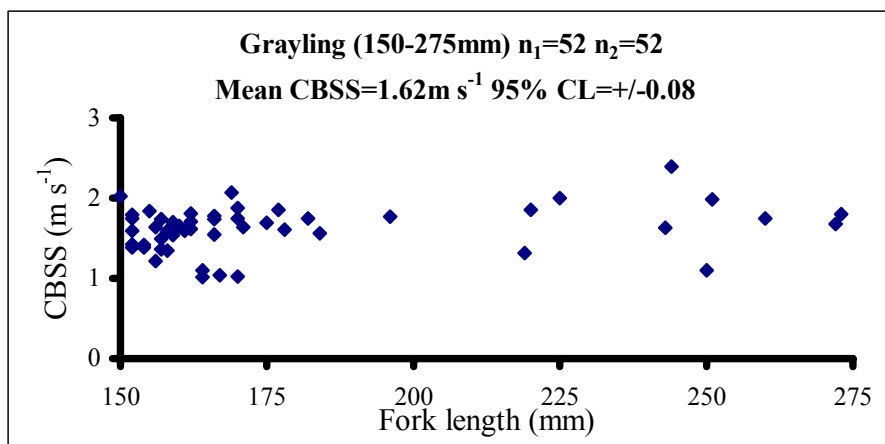
Figure 4.2.3e
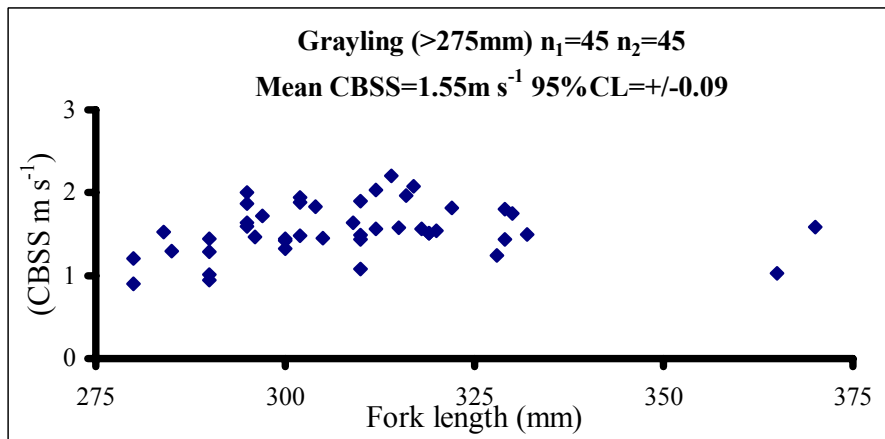
Figure 4.2.3f

Figures 4.2.3 d-f. Critical Burst Swimming Speeds of grayling at >15°C.
n_1 = no. of individual fish tested, n_2 = total no. of fish tested
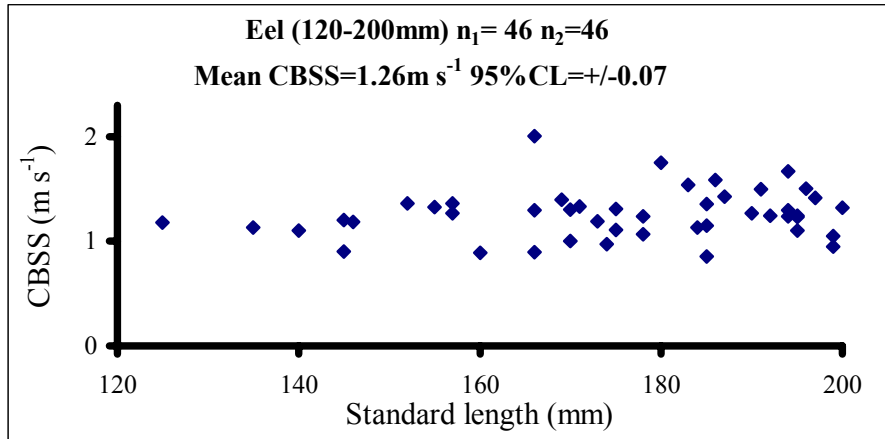
Figure 4.2.3g
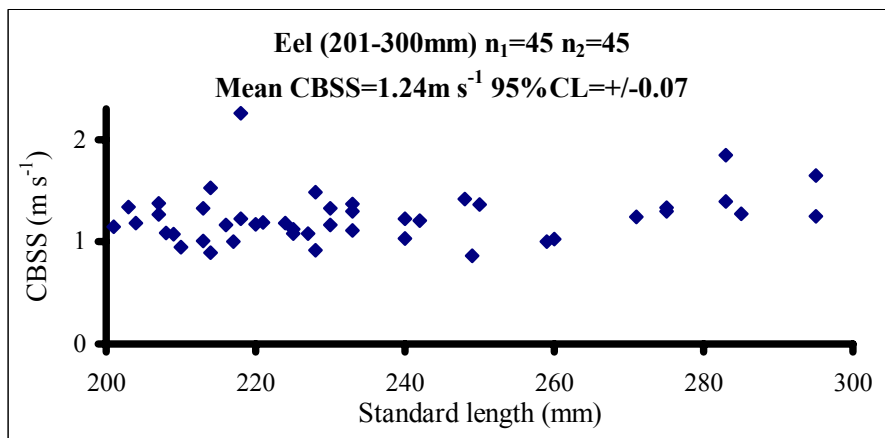
Figure 4.2.3h
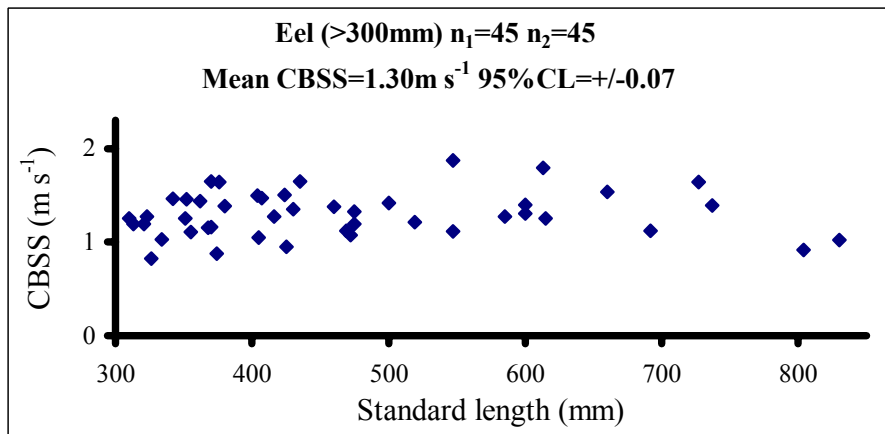
Figure 4.2.3i

Figure 4.2.3 g-i. Critical Burst Swimming Speeds of eels at >15°C.
n_1 = no. of individual fish tested, n_2 = total no. of fish tested

Bream (<100mm) n_1=78 n2=78
Mean CBSS=1.01m s^{-1} 95%CL=+/-0.03
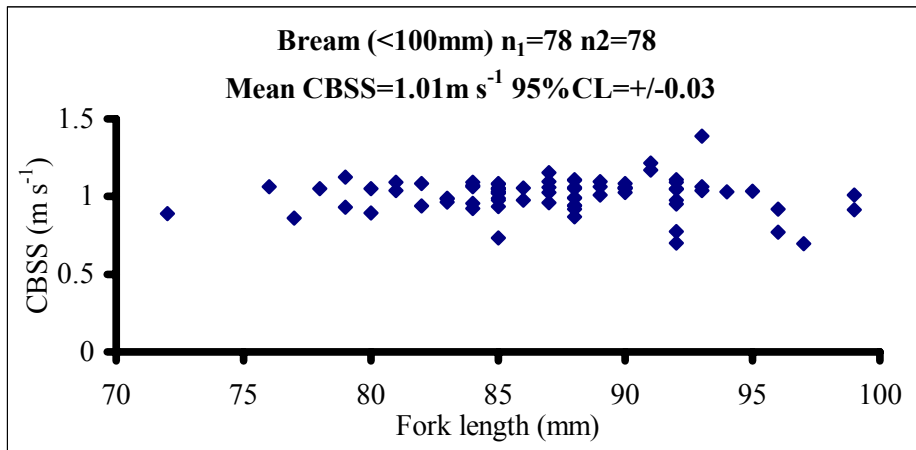
Figure AIII.3j.

Figure AIII.3j.   Critical burst swimming speeds of bream at >15°C. n_1 = no. of individual fish tested, n_2 = total no. of fish tested.

APPENDIX IV. Critical Burst Swimming Speed charts (data presented in body lengths per second).
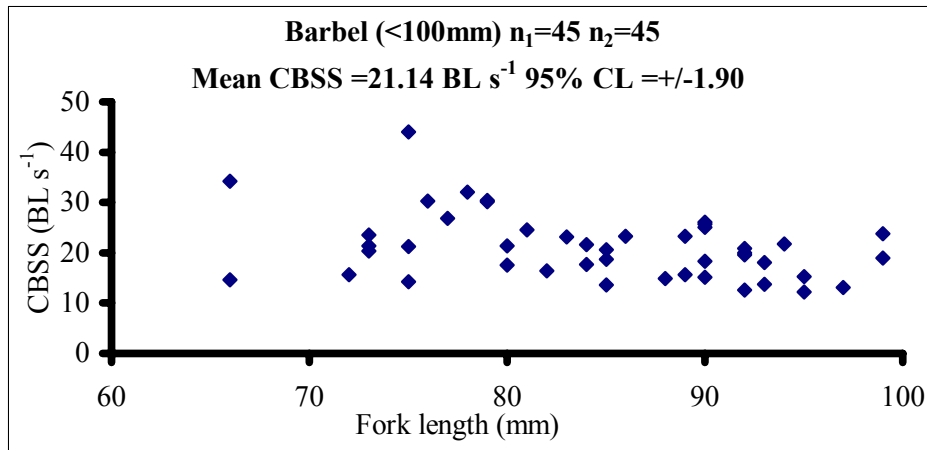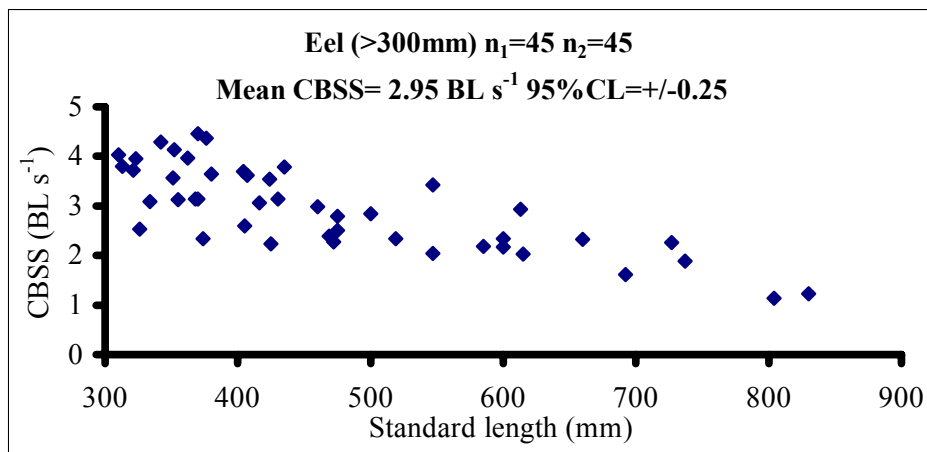

Figure AIV.1a.
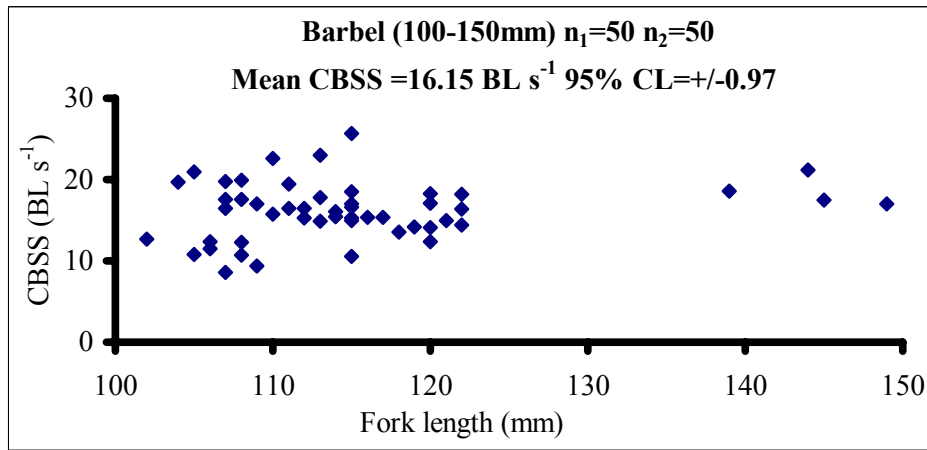
Figure AIV.1b
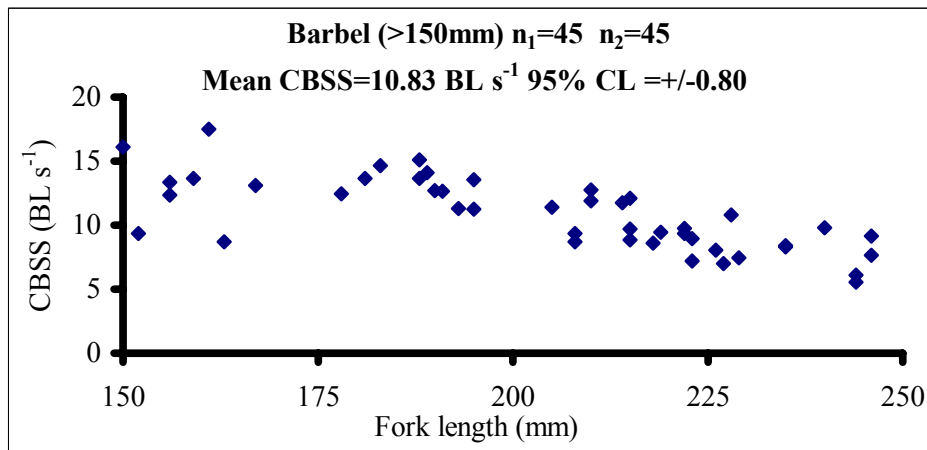
Figure AIV.1c.

Figures AIV.1a-c. Critical burst swimming speeds of barbel at 5-10°C.
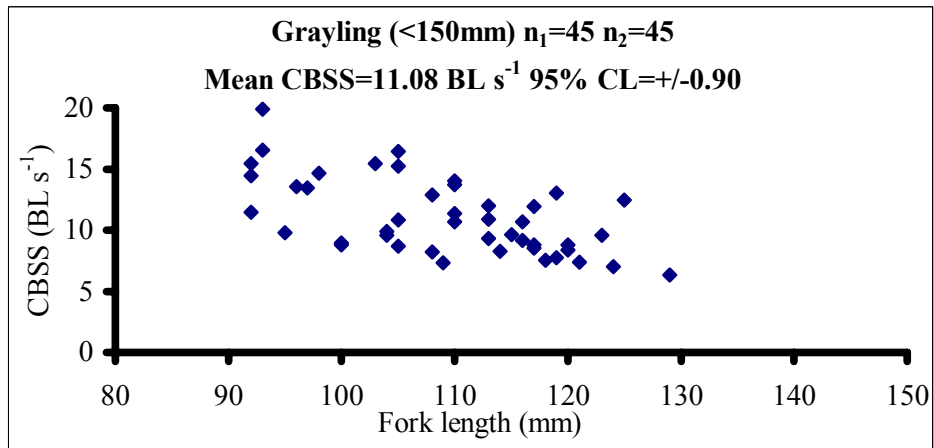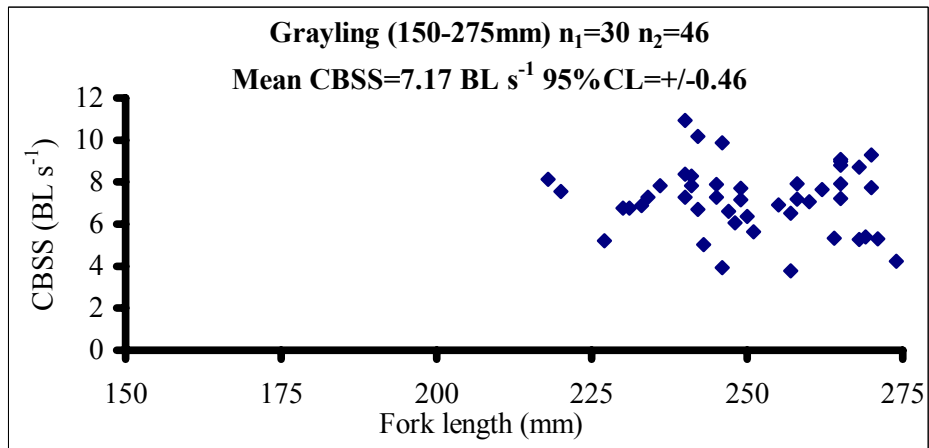
Figure AIV.1d

Figure AIV.1e.
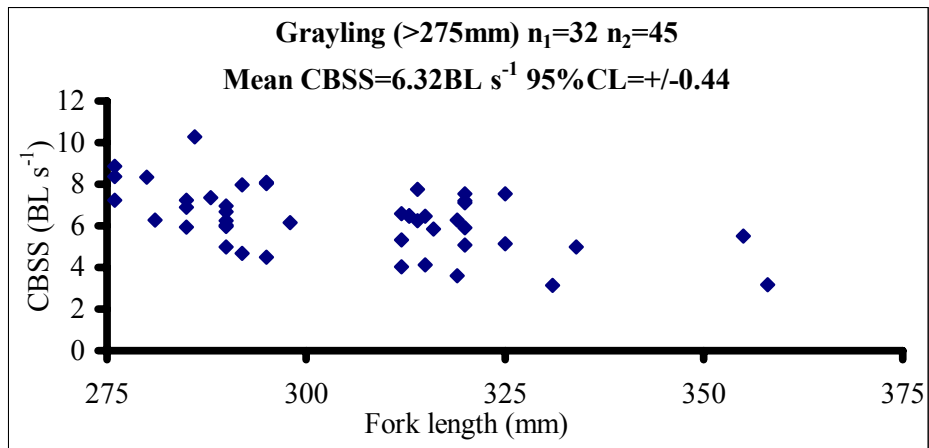
Figure AIV.1f.

Figures AIV.1d-f. Critical burst swimming speeds of grayling at 5-10°C.
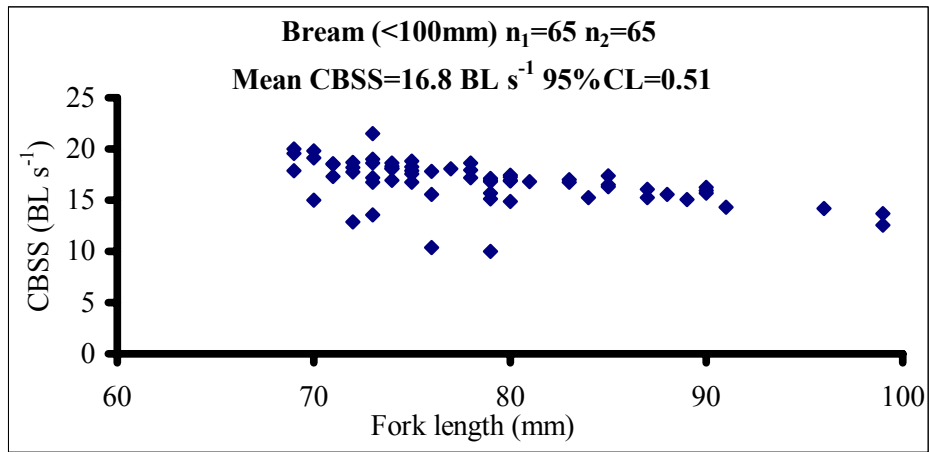
Figure AIV.1g.

Figure AIV.1g. Critical burst swimming speeds of bream at 5-10°C.
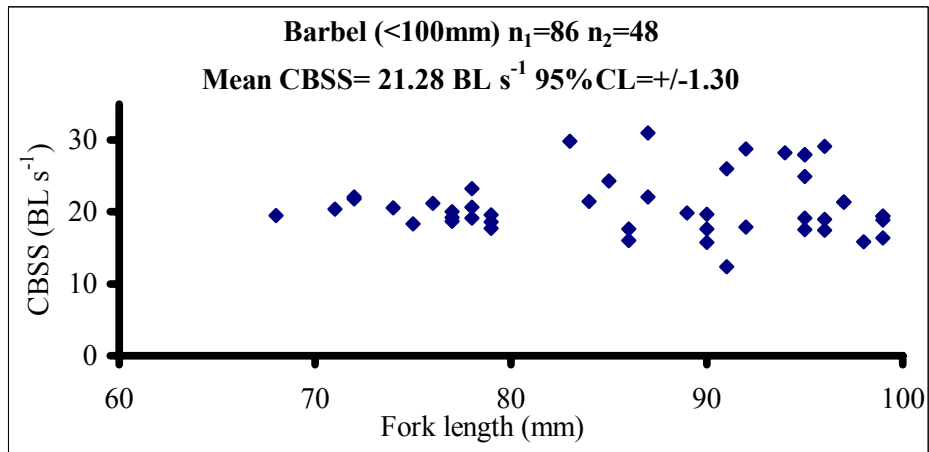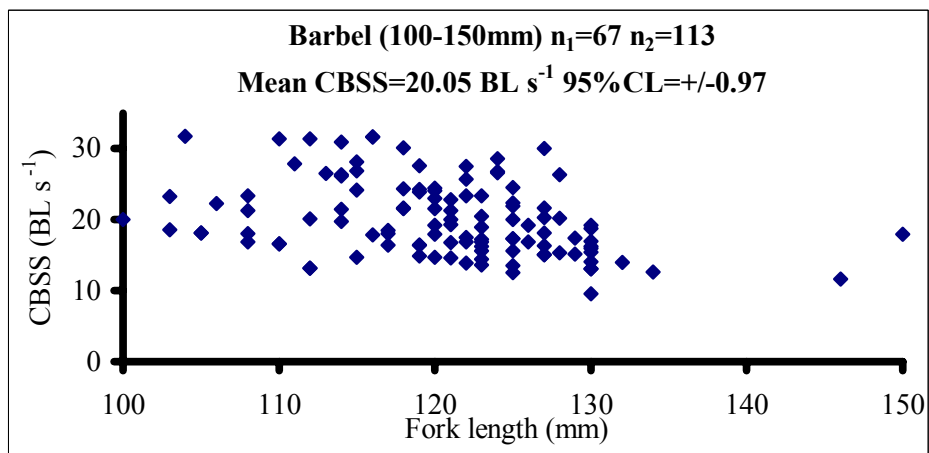
Figure AIV.2a.

Figure AIV.2b.
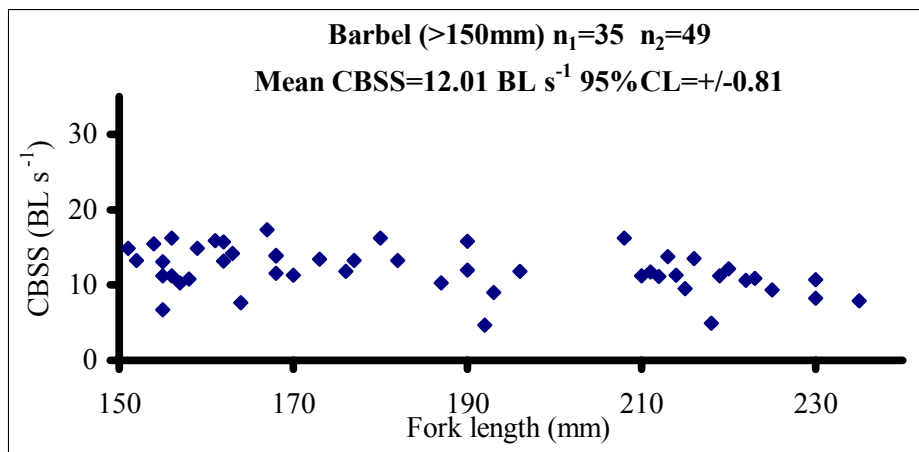
Figure AIV.2c.

Figures AIV.2a-c. Critical burst swimming speeds of barbel at 10-15°C.
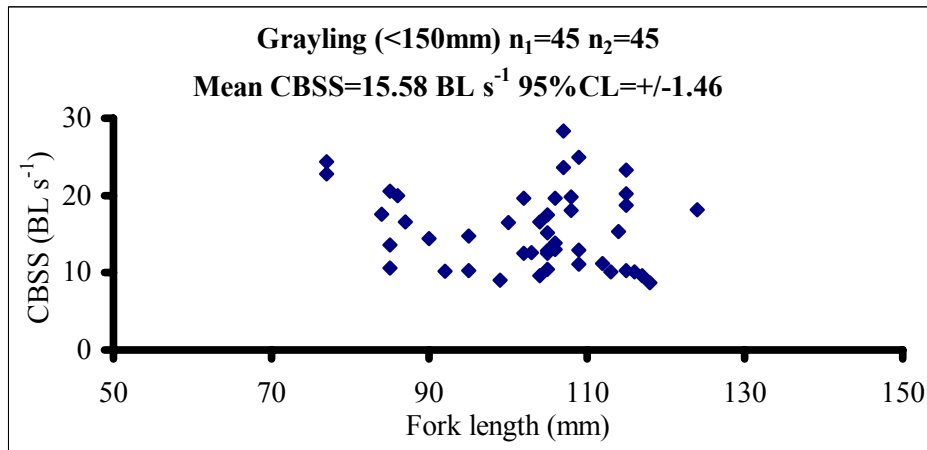
Figure AIV.2d.
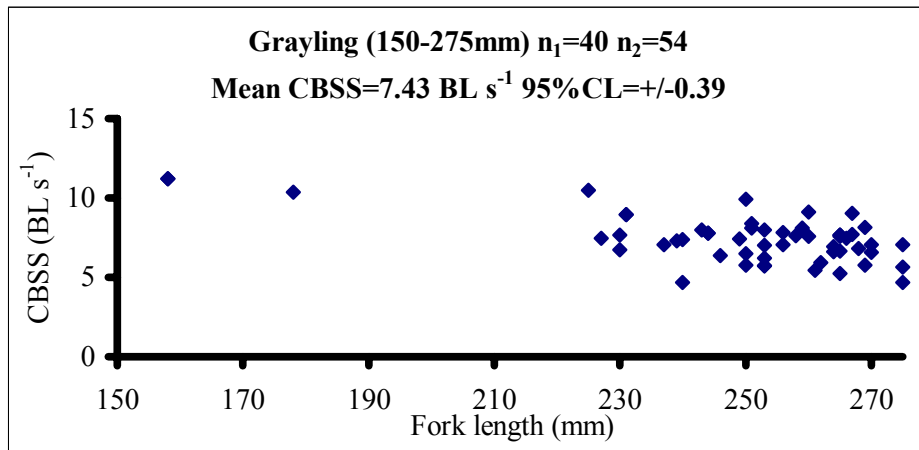
Figure AIV.2e.
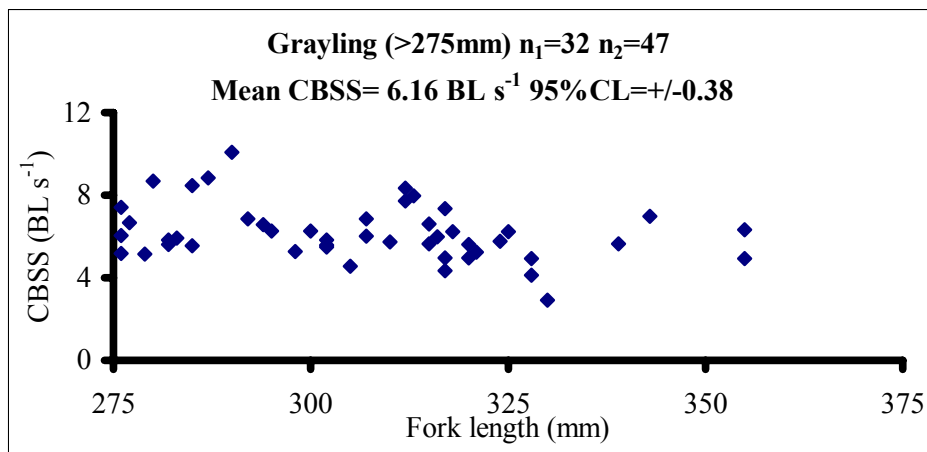
Figure AIV.2f.

Figures AIV.2d-f. Critical burst swimming speeds of grayling at 10-15°C.
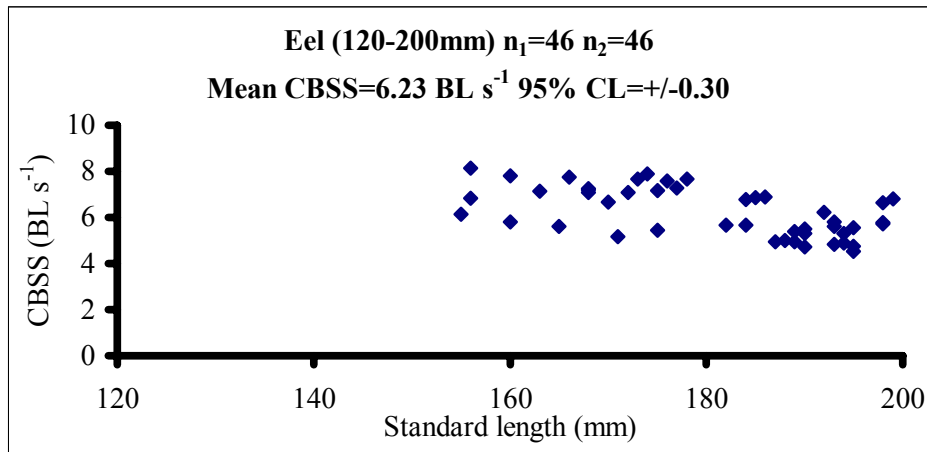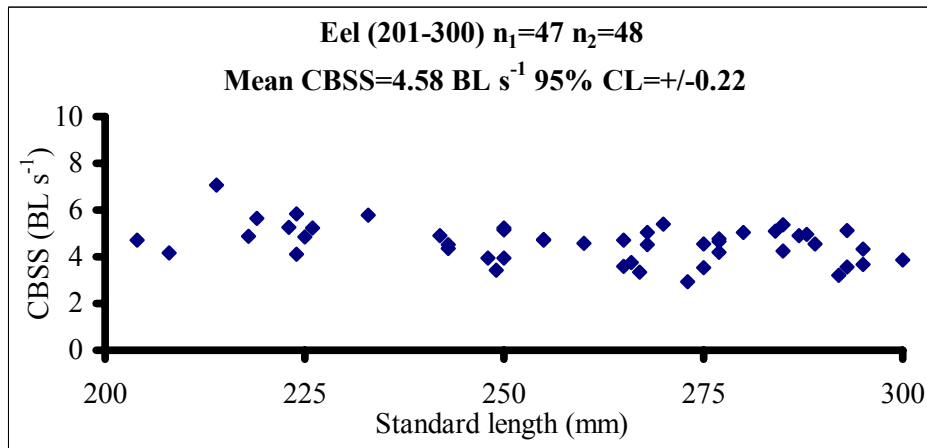
Figure AIV.2g.

Figure AIV.2h.
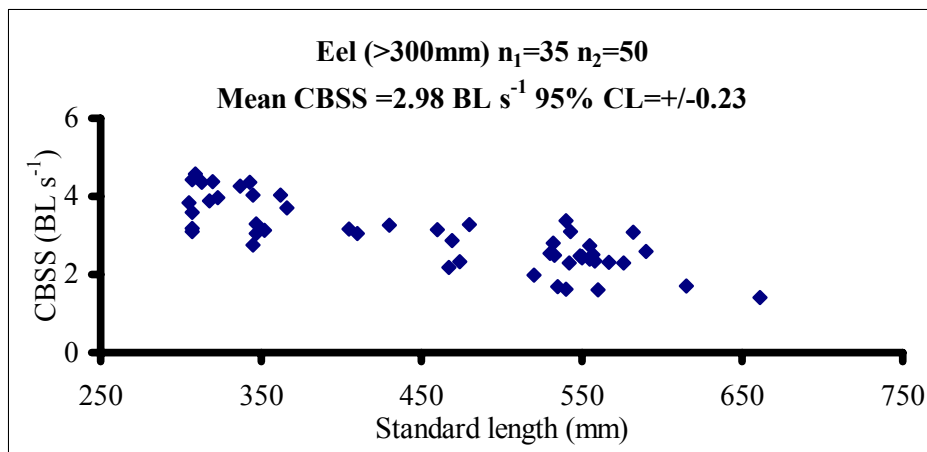
Figure AIV.2i.

Figures AIV.2g-i. Critical burst swimming speeds of eels at 10-15°C.

Bream (<100mm) n_1=45 n_2=45
Mean CBSS=14.57 BL s^{-1} 95% CL=+/-0.81
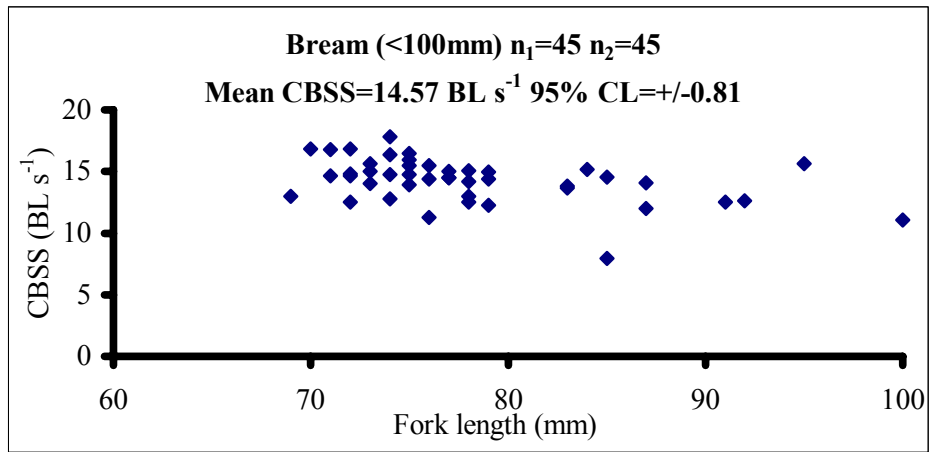
Figure AIV.2j.

Figure AIV.2j. Critical burst swimming speeds of bream at 10-15°C.
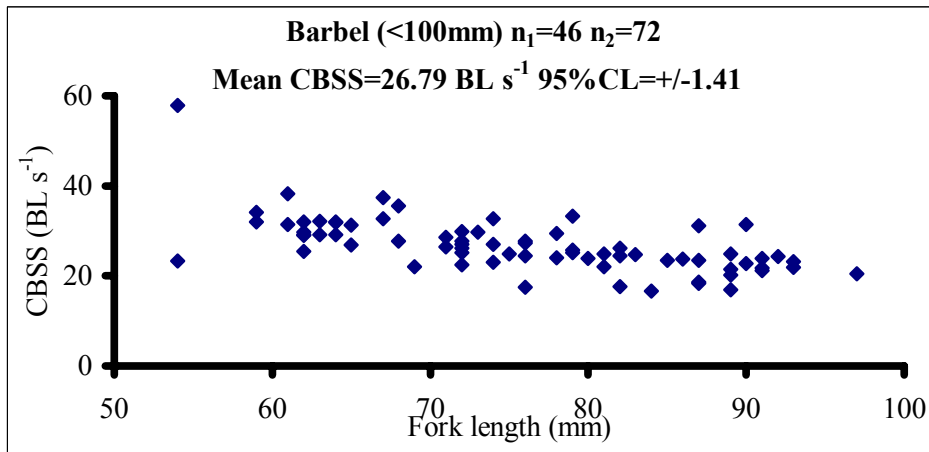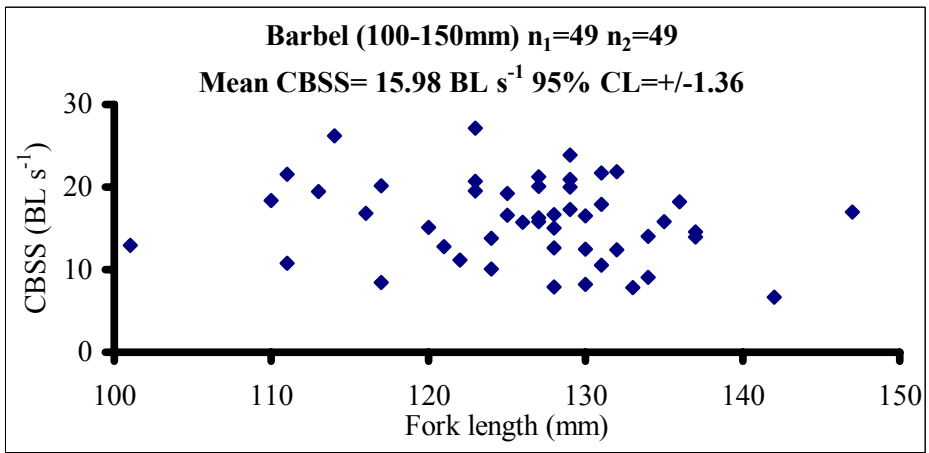
Figure AIV.3a.

Figure AIV.3b.
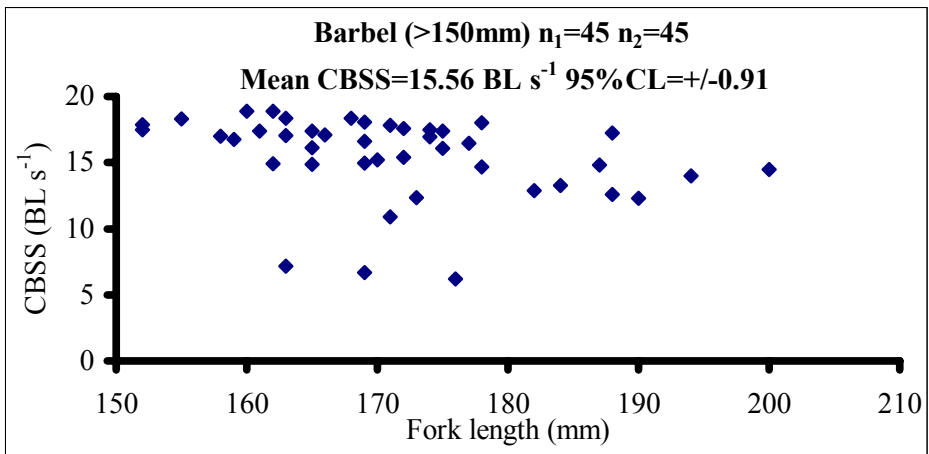
Figure AIV.3c.

Figures AIV.3a-c. Critical burst swimming speeds of barbel at 15-20°C.
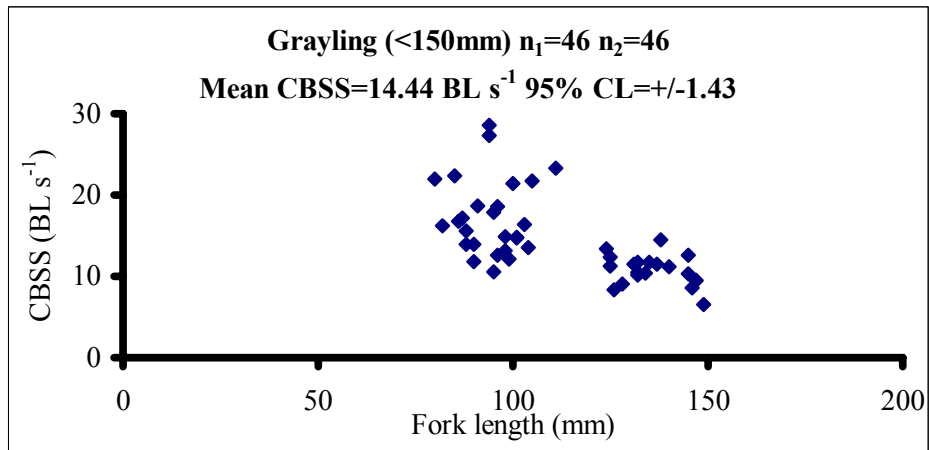
Figure AIV.3d.
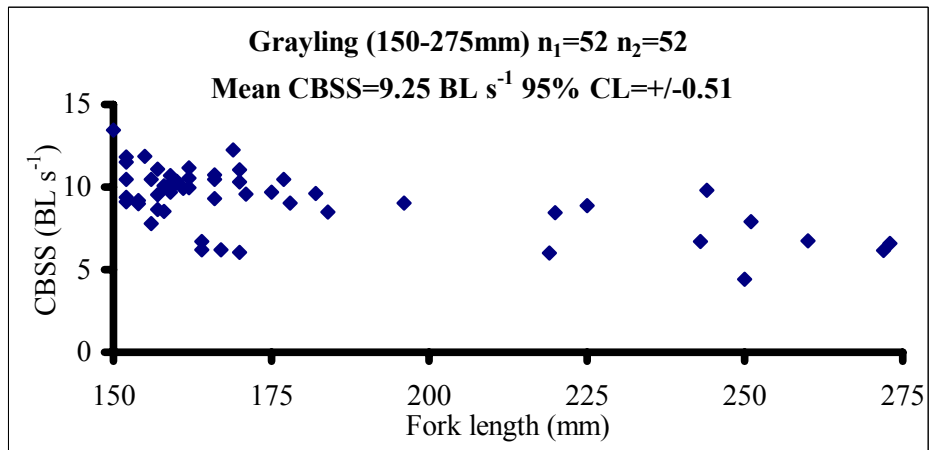
Figure AIV.3e.
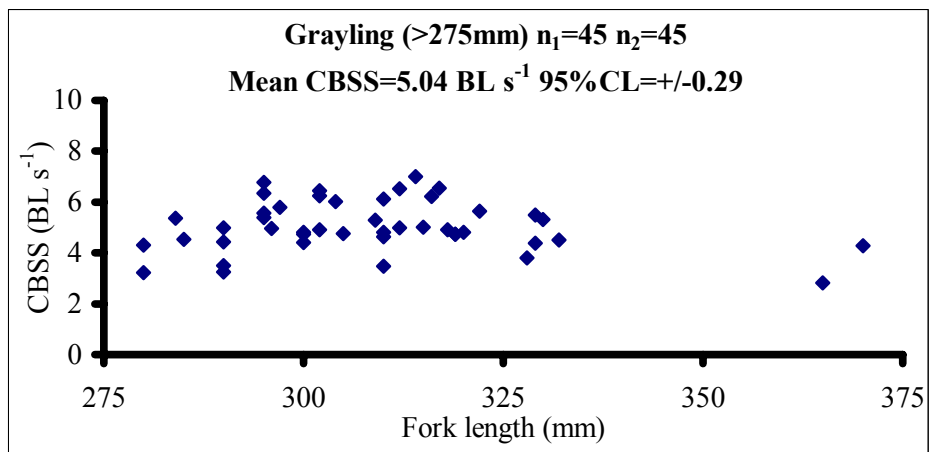
Figure AIV.3f.

Figures AIV.3d-f. Critical burst swimming speeds of grayling at 15-20°C.
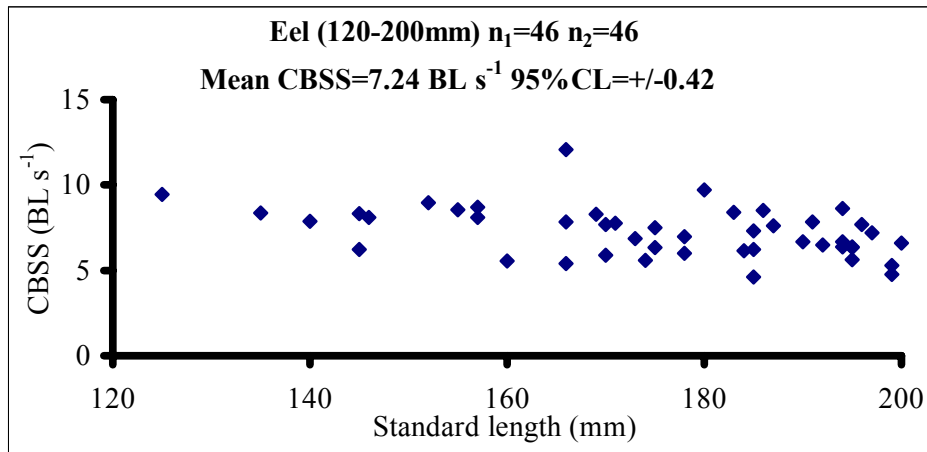
Figure AIV.3g.
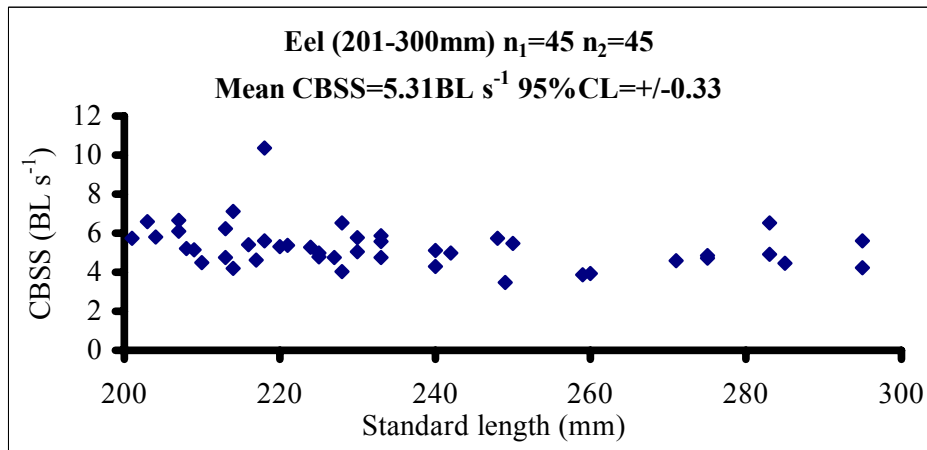
Figure AIV.3h.

Figure AIV.3i.

Figures AIV.3g-i. Critical burst swimming speeds of eels at 15-20°C.
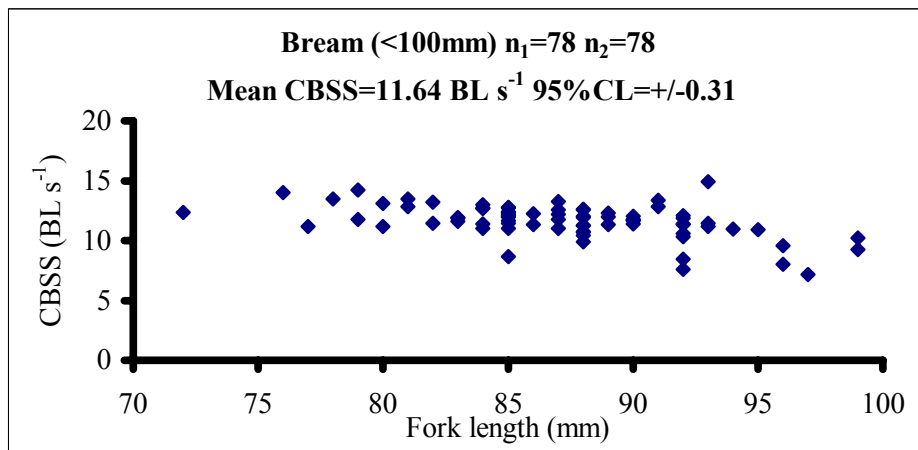
Figure AIV.3j.

Figure AIV.3j. Critical burst swimming speeds of bream at 15-20°C.

APPENDIX V. Mean CBSS summary graphs. (water velocity in BL s^{-1}).
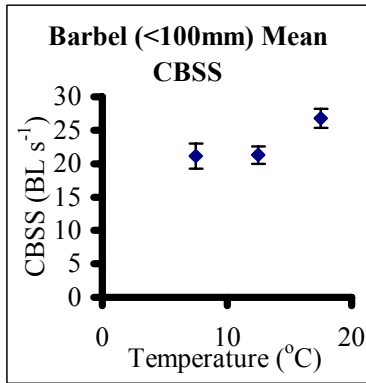
Figure AV.1a
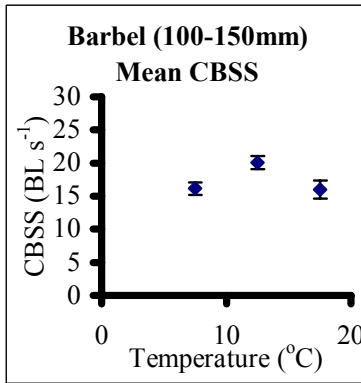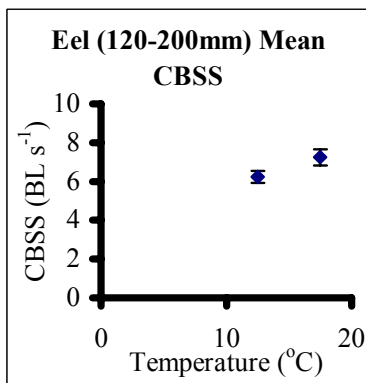

Figure AV.1b
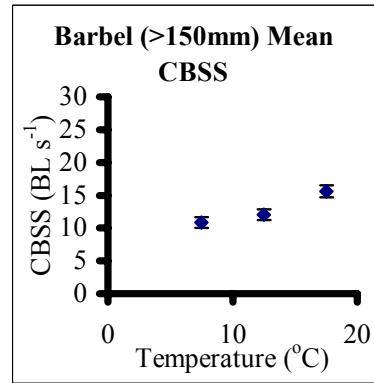
Figure AV.1c
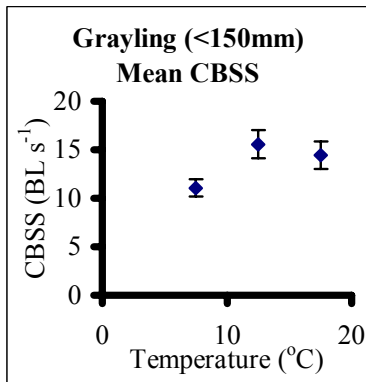
Figure AV.2a
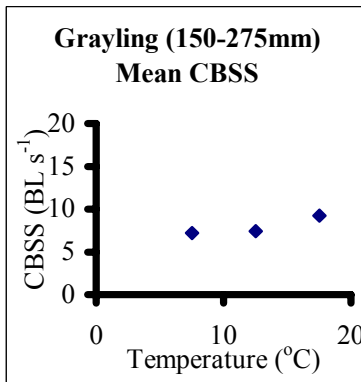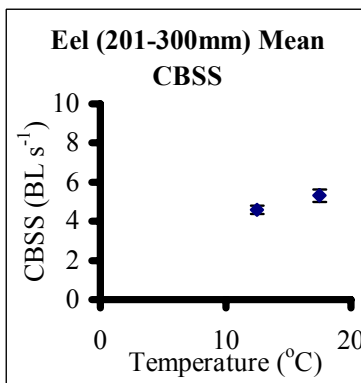

Figure AV.2b
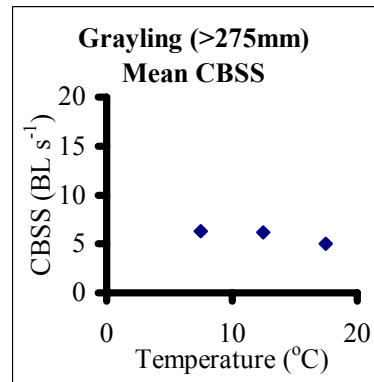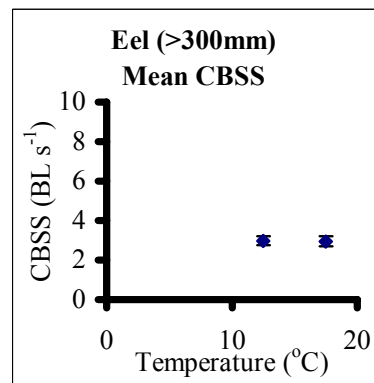

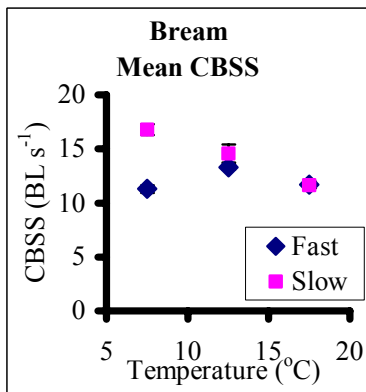Figure AV.2c

Figure AV.3a

Figure AV.3b

Figure AV.3c

Figure AV.4

Figures AV.1–AV.4. Mean CBSS graphs (water velocity in body lengths per second).

APPENDIX VI Extract from report on smelt (*Osmerus eperlanus*) swimming speed tests carried out on behalf of TWU.

1.   INTRODUCTION

This Appendix describes swimming speed trials of smelt carried out on behalf of Thames Water Utilities Ltd (TWU). TWU agreed that the data should be made available for use in SWIMIT v.2.0. A description of the source of fish, methods and experimental results is provided here.

2.   METHODS

2.1   Fish Collection, Handling and Husbandry

Smelt of a range of sizes (48-177 mm fork length) were collected from the cooling water intake of Barking power station, which is situated on the Thames Tideway. Initial attempts to collect live smelt were unsuccessful, with very high (90%+) initial mortalities. However, this problem ceased once river temperatures had fallen below 17°C. Once collected, the fish were transported in clean oxygenated water with a salinity of 6-10 ‰. Test fish were retained in a 5 m diameter indoor pool at Fawley Aquatic Research Laboratories, and held for a minimum of 3 days prior to testing. Salinity in the stock pool was maintained at 5 ‰ throughout. Although the unheated stock pool was situated indoors, it was subject to natural diel and seasonal fluctuations of light and temperature. A low-velocity circulation of water within the pool was provided by an external pump in order to exercise the fish. The water in the stock pool was changed as required, by partial replacement. Test fish were divided into two groups according to length, these being (<90 mm and ≥90 mm). The burst swimming capacity of fish from each of these two categories was tested within two different temperature ranges (<12°C and ≥12°C). Endurance swimming tests were also conducted at the seasonal ambient temperature, and results are in the same ranges.

A few mortalities of smelt occurred, mainly during transportation and in the first few days after collection. When the fish had settled, mortalities ceased. Feeding the fish proved difficult. Several live foods were tried, such as sand smelt, shrimps, ragworm and maggots, but the only food eaten were sand hoppers, which were collected from a shingle beach and fed to the fish either by hand or drip feeder.

2.2   Swimming Test Apparatus

The apparatus and protocols used during this study are consistent with those used for Phase 2 of the R&D project on 'Swimming Speeds in Fish'.

3. RESULTS

3.1   Burst swimming

Critical burst swimming speeds were calculated for 45 small and 45 large smelt in two temperature categories (Figures 3.1a-d). Critical burst swimming speeds for smelt were

similar across sizes and temperatures, generally being between 1.0 and 1.2 m s^{-1} throughout. Within each temperature band the mean CBSS was not significantly different between length classes at the 95% confidence level (Figure 3.2; Table 3.1).
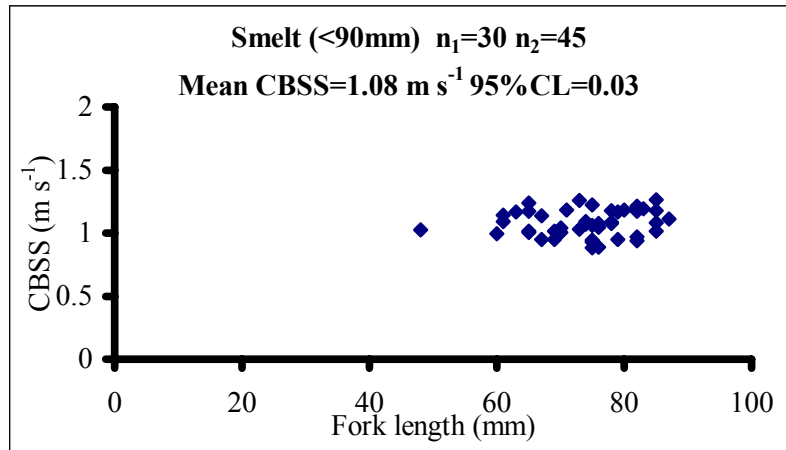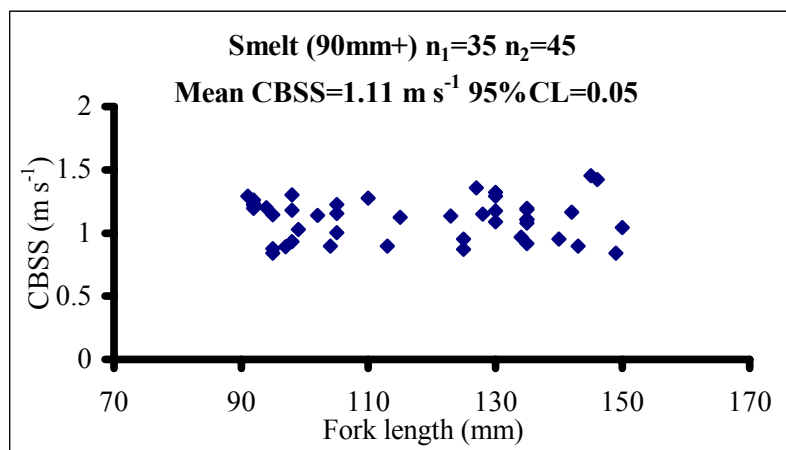

Figure 3.1a.

Figure 3.1b.

Figure 3.1a & b. Critical burst swimming speeds of smelt at >12 °C. n_1 = number of individual fish used for tests, n_2 = total number of fish tested.
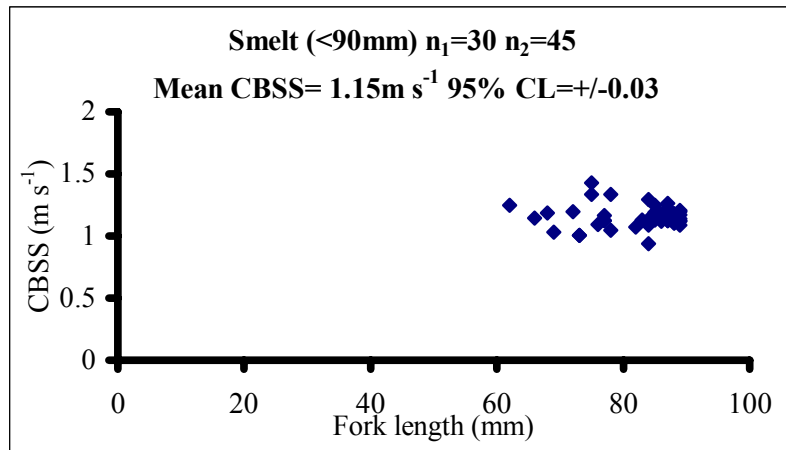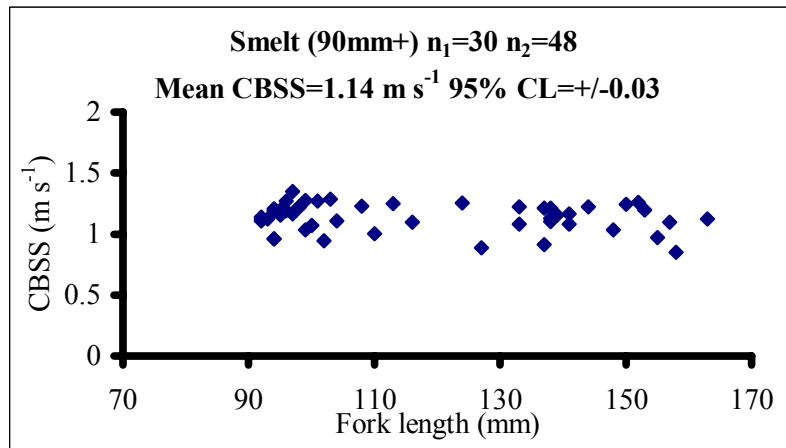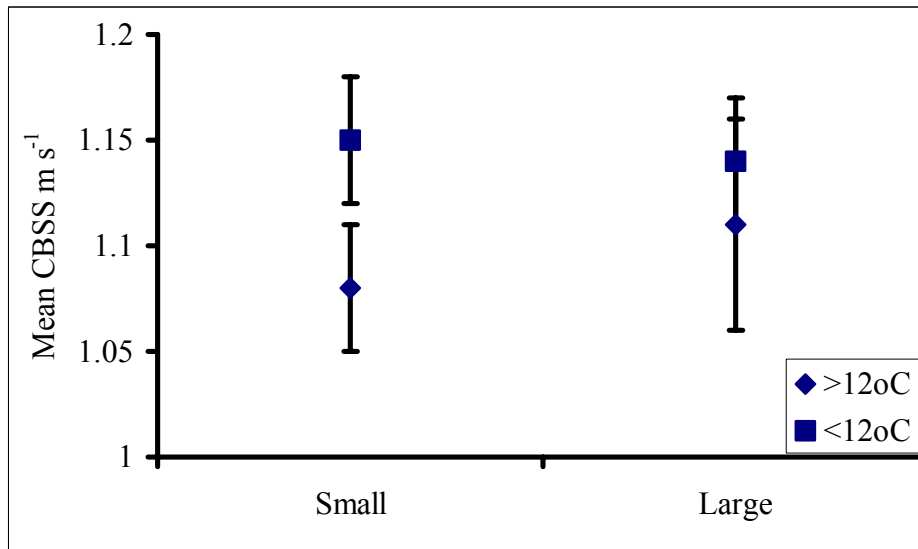
Figure 3.1c.

Figure 3.1d.

Figure 3.1c.&d. Critical burst swimming speeds of smelt at <12 °C. n_1 = number of individual fish used for tests, n_2 = total number of fish tested.

Figure 3.2. Mean critical burst swimming speeds of two sizes of smelt at two temperatures. Error bars are 95% confidence limits.

Table 3.1 Summary of mean CBSS and 95% confidence limits for smelt

Temp. (^{o}C)	Size Class	Mean CBSS (m s^{-1})	95% C.L.
<12	Small	1.15	0.03
	Large	1.14	0.03
>12	Small	1.08	0.03
	Large	1.11	0.05

3.2   Endurance swimming

Performance in the endurance tests improved both with increasing fish length, and with increasing temperature (Figures 3.3 a-d). The threshold at which median endurance fell below 200 minutes for both smelt sizes was between 0.35 and 0.4 m s^{-1} at >12 ^{o}C, and between 0.3 and 0.35 m s^{-1} at <12 ^{o}C (Tables 3.2a & b).

Composite curves, showing both endurance and burst fatigue times for two sizes of smelt at two temperatures were plotted on a logarithmic scale (Figure 4; after Beamish, 1978). These data demonstrate that fatigue times of smelt at a water velocity of 0.3 m s^{-1} are in excess of 100 minutes, whereas at 0.6 m s^{-1} fatigue times are between 1 and 2 minutes.
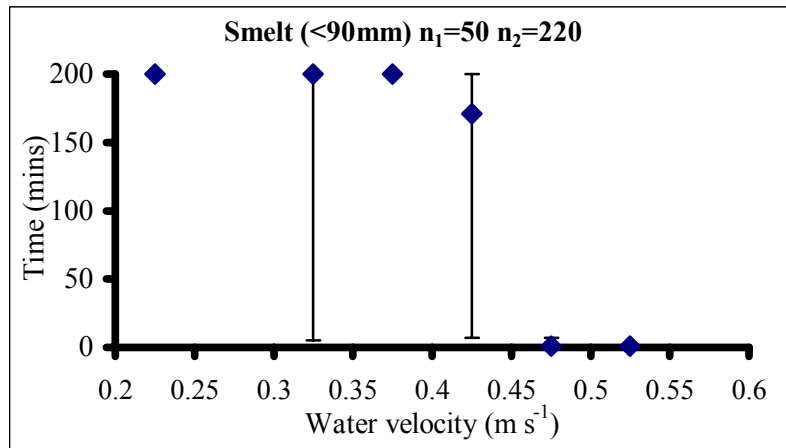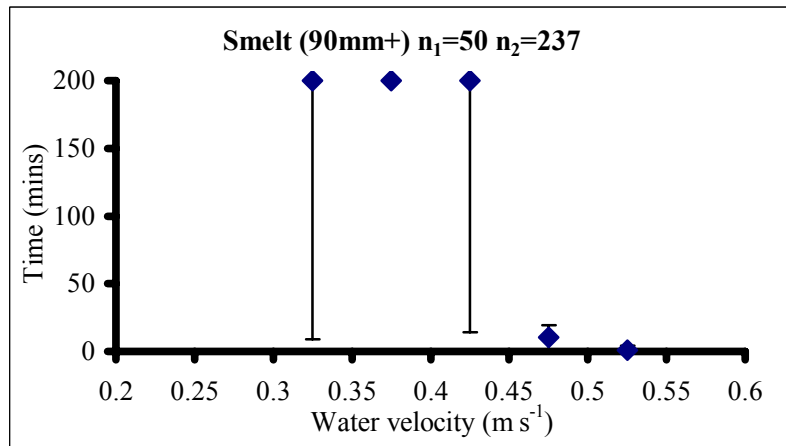
Figure 3.3a.

Figure 3.3b.

Figure 3.3a.&b. Median endurance times for smelt at >12°C. n_1 = number of individual fish used for tests, n_2 = total number of fish tested. Error bars are upper and lower quartiles.
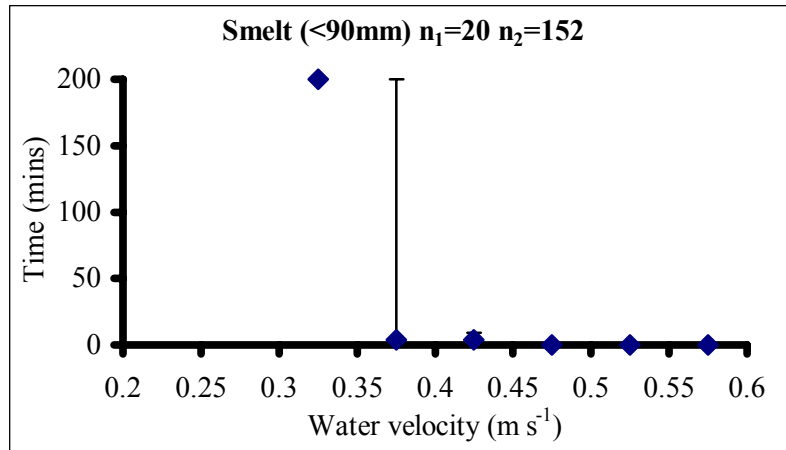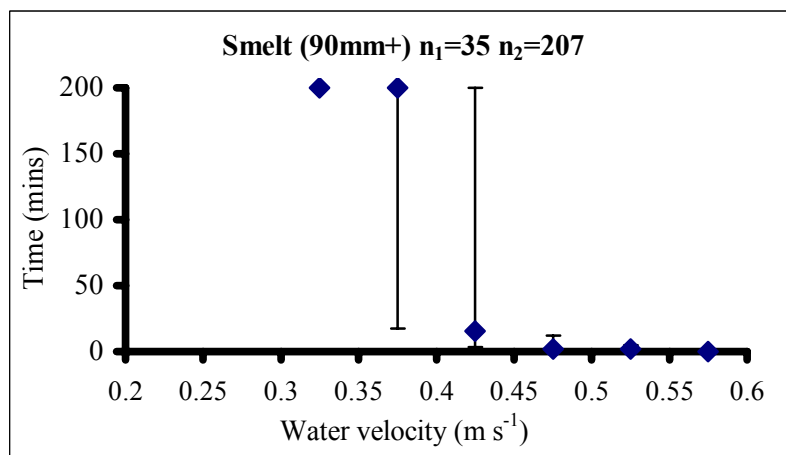
Figure 3.3c.

Figure 3.3d.

Figure 3.3c.&d. Median endurance times for smelt at <12°C. n_1 = number of individual fish used for tests, n_2 = total number of fish tested. Error bars are upper and lower quartiles.
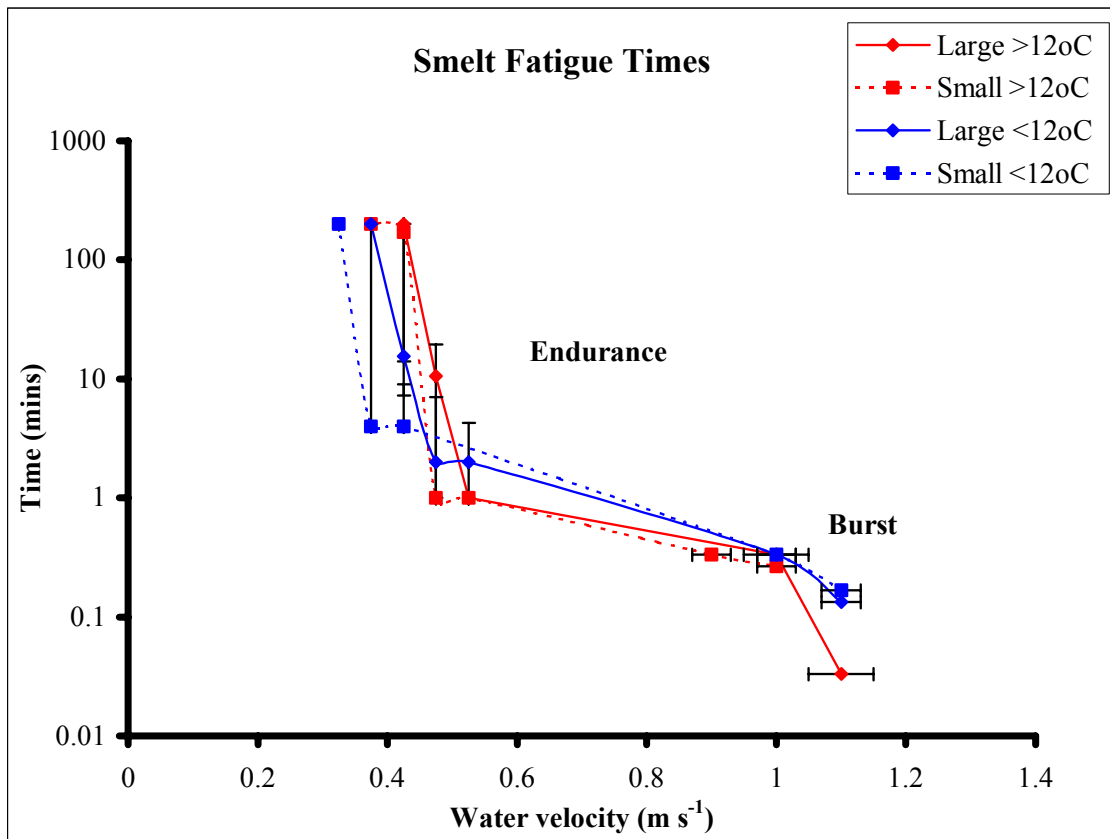
Figure 3.4. Smelt fatigue times at different water velocities. Vertical error bars on median endurance swimming data points represent upper and lower quartiles. Horizontal error bars on mean burst swimming data points represent 95% confidence limits.
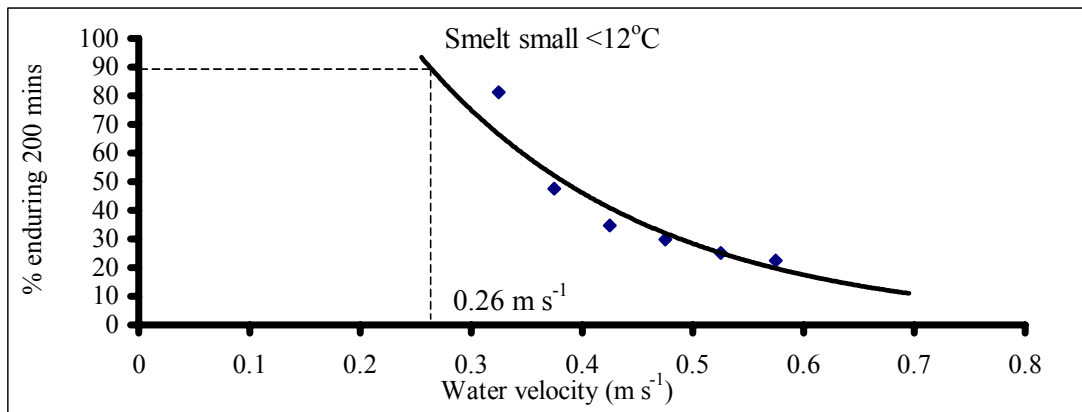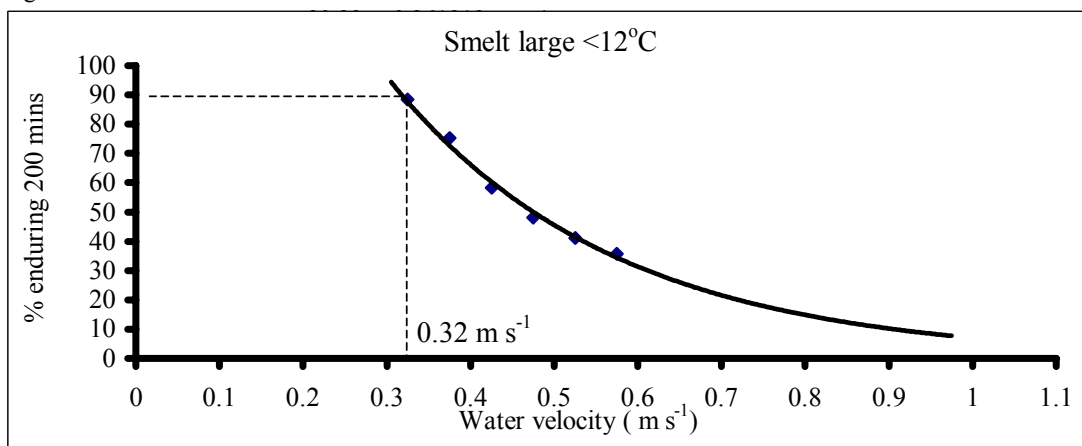
Figure 3.5a.

Figure 3.5b.

Figure 3.5 a & b. Percent of smelt tested which endured 200 minutes. Dotted line denotes the maximum speed at which 90% of fish would be able to swim for 200 minutes or more.
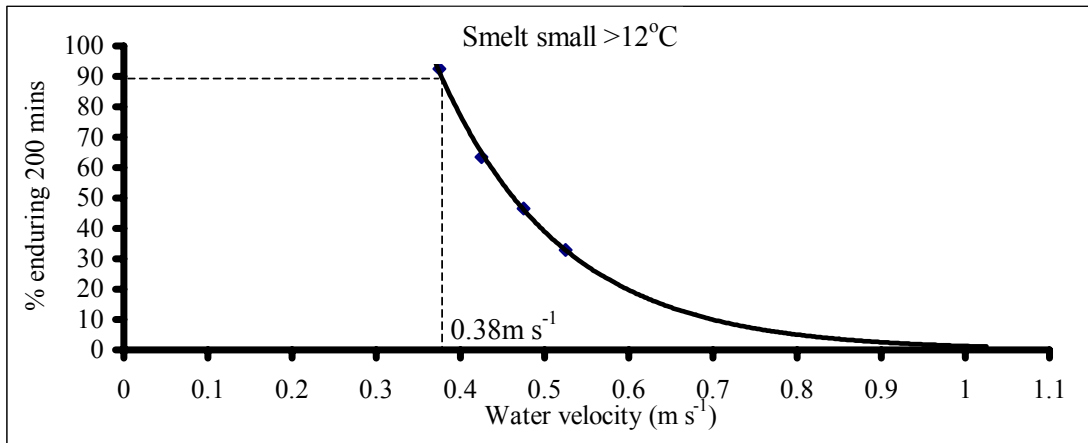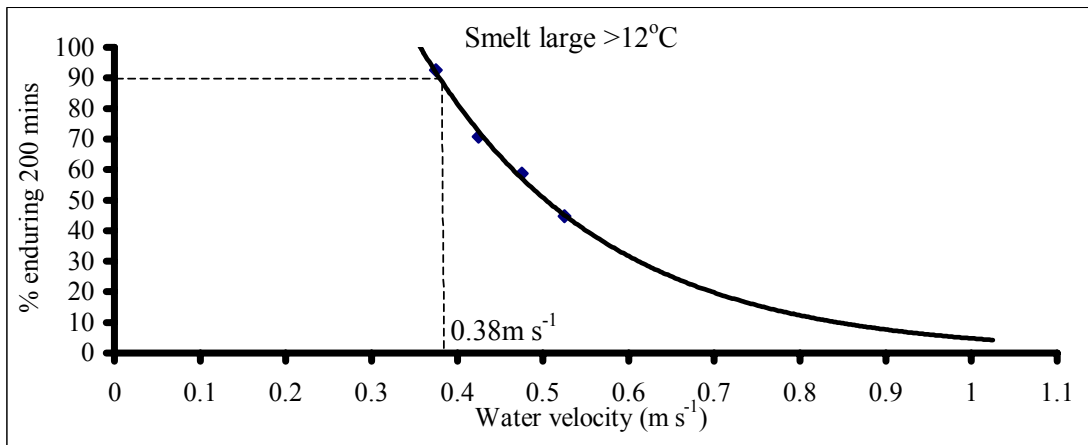
Figure 3.5c.

Figure 3.5d.

Figure 3.5 c & d. Percent of smelt tested which endured 200 minutes. Dotted line denotes the maximum speed at which 90% of fish would be able to swim for 200 minutes or more.

4. DISCUSSION

In spite of the initial problems sourcing, collecting, transporting and keeping live smelt, successful experiments were conducted with two size groups of smelt, within two temperature categories.

Critical burst swimming speeds showed little variation with size or temperature, and were generally between 1 and 1.2 m s^{-1}. This is in contrast to the results achieved in trials carried out on 90 smelt from the Elbe estuary (Germany) (Sprengel and Lüchtenberg, 1991). Their study suggested the critical burst swimming speed of a 15 cm smelt to be 0.49 m s^{-1} at 17°C. In view of our findings in the present study, their results appear to underestimate the burst swimming capability of smelt by a factor of two. The discrepancy may reflect differences in the condition of the fish, insufficient acclimation time after collection, and the test method itself, which used a circular testing tank with maximum flow velocity of 1.1 m s^{-1}. Longer acclimation times and a linear testing tank are likely to make the results from our experiments more reliable. Infections by endoparasites in the muscles have also been shown to significantly reduce smelt swimming speeds, causing them to be susceptible to entrainment into cooling water intakes (Sprengel & Lüchtenberg, 1991). In this experiment, no post-mortems were carried out after testing, therefore results encompass all fitness levels and are representative of the smelt in the Beckton area. These results demonstrate that, given an appropriate repellent stimulus, smelt of all sizes tested would be able to burst-swim fast enough to avoid entrainment where intake velocities did not exceed about 1 m s^{-1}.

The endurance swimming capacity of smelt increased with both increasing length and temperature. The threshold values at which median endurance first falls below 200 minutes ranges from 0.35 m s^{-1} for small smelt at less than 12°C to 0.45 m s^{-1} for larger smelt at the higher temperature.

5. ACKNOWLEDGEMENTS

6. REFERENCES

Beamish, F. W. H. (1978). Swimming capacity. In: Fish Physiology. W. S. Hoar. London, Academic Press: 101-187.

Sprengel, G. & Lüchtenberg, H. (1991). Infection by endoparasites reduces maximum swimming speed of European smelt (*Osmerus eperlanus*) and European eel (*Anguilla anguilla*). Diseases of Aquatic Organisms 11, 31-35.