

~~**JTIR00030**~~



Navigation impacts on freshwater fish assemblages: the ecological relevance of swimming performance

C. Wolter & R. Arlinghaus

Leibniz Institute of Freshwater Ecology and Inland Fisheries, Department of Biology and Ecology of Fishes, P.O. Box 850 119, 12561 Berlin, Germany (Phone: +49 30 64181633; Fax: +49 30 64181750; E-mail: wolter@igb-berlin.de)

Accepted 16 May 2003

Contents

Abstract	page 63
Introduction	64
Effects of navigation on fish	66
Direct impacts	
Indirect impacts	
Swimming performance of fish	68
Ecological relevance of swimming performance	
Critical and burst swimming speed of freshwater fishes	
Navigation-induced physical forces	72
Navigation-induced habitat bottleneck hypothesis (NBH)	74
Primary stressors	
Secondary stressors	
Empirical evidence	
Conclusion	
Prospect for the future	78
Acknowledgements	78
References	79
Appendix	85

Key words: anthropogenic impact, ecosystem management, freshwater fish larvae, inland waterway, navigation bottleneck hypothesis, NBH, sustainability

Abstract

Waterways provide many ecological and social services, such as water supply, navigation, freshwater reservoirs for aquatic organisms, recreation, and fisheries. However, in heavily developed waterways, the diversity and productivity of fish assemblages typically become reduced, mainly due to migration barriers, pollution, habitat loss, and biotope simplification. Additionally, navigation may directly or indirectly reduce fish assemblages, amplifying the effects of habitat destruction. This study summarizes navigation impacts to improve the evaluation of direct navigation effects on fish assemblages. Literature on hydraulic forces created by moving tows was reviewed to compare the pressures induced by shipping with the biological capabilities of fish, especially with their swimming speeds. Available studies of swimming performance of freshwater fishes were compiled to develop general models of length-specific burst, as well as critical swimming speeds. Models regressing total length on burst and critical swimming speeds were highly significant. Linking applied hydrology and hydraulic engineering with fish ecology and physiology, absolute speed was concluded to be the best predictor for thresholds and limitations of habitat use.

by fish. A navigation-induced habitat bottleneck hypothesis (NBH) was inferred from the threshold flow velocity, determining habitat availability for fish. According to the NBH presented here, swimming performance of juvenile freshwater fish is the major bottleneck for fish recruitment in waterways, as a result of their inability to withstand bank-directed navigation-induced physical forces. In essence, under common navigation conditions, with respect to inland waterway morphology, channel cross section, vessel speeds, and dimensions of commercial vessels, the navigation-induced return currents along the shore are usually around 0.8 m s^{-1} ($0.7\text{--}1.0 \text{ m s}^{-1}$) accompanied by a $0.1\text{--}0.3 \text{ m}$ drawdown. Under such conditions, the proposed threshold for small fish survival was estimated to be 147 mm total length at critical swimming performance ($>20 \text{ s}$ — 60 min without fatigue) and 47 mm at burst performance ($<20 \text{ s}$). These theoretical findings were supported by empirical studies of fish recruitment in waterways. The strong dependence of fish recruitment on hydraulic forces opens up possibilities of formulating suitable criteria for safe ship operation (speed and distance to bank), as well as for effective fairway management (construction and maintenance) and sustainable fish conservation (species and production). A more ecologically orientated hydraulic engineering will not constrain commercial navigation and their socioeconomic benefits, but it will substantially enhance fish recruitment in waterways and their ecological sustainability, for the overall benefit of fish, fisheries, and society.

Introduction

At present, all of the earth's ecosystems have to be considered human impacted (Vitousek et al., 1997). Therefore, to a certain degree, anthropogenically induced environmental changes have to be accepted as integral parts of the ecosystem, as they tend to be generalized in their effects. At the same time, the human population is steadily growing and urbanization is a common trend worldwide. Indeed, many people believe that, in particular, urban environmental conditions are deteriorating and the conditions of waterways, such as regulated rivers and canals, are high on their list of worries (Karr and Chu, 1999). Worldwide there are $500,000\text{--}600,000 \text{ km}$ navigable inland waterways. Today, the existing network of waterways is half the length of the rail network and will continue to grow (Kubec and Podzimek, 1996). Global waterway traffic is concentrated within four areas: (1) Western and Central Europe, with more than $33,300 \text{ km}$ of inland waterways, (2) the territory of the former USSR with $144,500 \text{ km}$ navigable inland waterways, (3) USA with $41,403 \text{ km}$, and (4) the Far East and China, with more than $155,000 \text{ km}$ of inland waterways (Kubec and Podzimek, 1996). In total more than four billion tonnes of various goods are carried by ships on inland waterways each year and the trend is rising (Kubec and Podzimek, 1996; Justen, 2002; Sparks Companies, 2002). Shipping goods over long distances in regulated rivers and canals accounts for only around 7% of all CO_2 emission of the transport sector (European Commission, 2001; Graßl et al., 2002). Thus, among all transport modes, inland navigation is currently considered

the most environmentally sound and most sustainable transport form, because increasing traffic and fossil fuel combustion were identified as major sources of greenhouse gas emissions causing the threats of global warming (United Nations, 1997; Colville et al., 2001; European Commission, 2001). According to a navigation study for the Upper Mississippi River—Illinois Waterway System, the commercial navigation traffic will increase 25% to 100% over the 1992 baseline data within the next 50 years (Bartell and Campbell, 2000). At the same time, it was estimated by the European Commission (2001) that the capacity of European inland waterways is considerably underused in terms of infrastructure and vessels, and has to be reinforced. As a result, one of the main points of the action programme for the trans-European transport network is the improvement of a waterway linking the North Sea with the Black Sea (European Commission, 2001). The likely increase of traffic on waterways will be accompanied by increased power of towboats, size of barges, and number of barges transported together (e.g. Bartell and Campbell, 2000; Hüsiger et al., 2000).

Waterways, however, do not only serve navigation purposes. At the same time, they are important freshwater reservoirs and provide habitats for many freshwater organisms (such as fish), allow for intensive recreational activities and inland fisheries, and may serve in conservation strategies for biotope connection, i.e. connect subpopulations of species in fragmented habitats. However, fish assemblages have dramatically changed due to migration barriers and river regulation for navigation purposes, and the effects of dredging, straightening and shoreline embankments. The basic cause-effect-relationship is

always similar: habitat fragmentation, simplification or loss, especially loss of spawning and nursery habitats for migratory and riverine fish species, leading to decreasing species numbers, diversity and productivity (e.g. Petts, 1985; Gore and Petts, 1989; Petts et al., 1989; Boon et al., 1992; Lelek and Buhse, 1992; Schiemer et al., 1994; Wolter and Vileinskas, 1997; Cowx and Welcomme, 1998; Simon, 1999; Wolter, 2001a,b). However, as a vessel navigates through a waterway, it generates hydraulic disturbances in the form of waves and currents, mainly drawdown, return current, slope supply currents, wash waves, and propeller jet. Thus, in addition to the indirect effects of "navigation" on fish assemblages, direct negative effects on fish caused by navigation-induced shear stress, shipwaves, drawdown, dewatering, backwash, and return currents have been commonly proposed (Holland and Sylvester, 1983; Holland, 1986; Nielsen et al., 1986; Pygott et al., 1990; Odom et al., 1992; Zauner and Schiemer, 1992, 1994; Wolter and Vileinskas, 1997; Jude et al., 1998; Killgore et al., 2001; Gutreuter et al., 2003), but rarely tested *in situ* (Mueller, 1980; Holland, 1986; Odom et al., 1992; Gutreuter et al., 2003) with partially contradictory results documenting impacts (Holland, 1986) or no impact (Odom et al., 1992). More often possible environmental effects of commercial navigation traffic have been estimated indirectly from observed fish assemblage changes (Jackiviez and Kuzminski, 1973; Liddle and Seorgie, 1980; Holland and Sylvester, 1983; Nielsen et al., 1986; Brookes and Hanbury, 1990; Adams, 1993; Murphy et al., 1995; Wolter and Vileinskas, 1997; Jude et al., 1998; Arlinghaus et al., 2002b). The direct effects of shear forces, waves and currents created by moving vessels on fish can be expressed as kills or injuries due to impact against the substrate or the vessel hull, and stranding out of water.

On the other hand, the physical forces during the passage of a vessel have been quantified by civil engineers in inland waterways for years to ensure navigation in general (e.g. Kuo et al., 1989; Maynard and Martin, 1997; Oebius, 2000a), increase the stability of embankments (e.g. Bhowmik et al., 1995; Daemrich et al., 1996; ASCE Task Committee, 1998; Thornton et al., 2000; Bauer et al., 2002) and waterways (e.g. Hochstein and Adams, 1989; Kuo et al., 1989; Sorensen, 1997; Fuehrer, 1998; Maynard, 1999; Oebius, 2000b), determine critical tow speeds (e.g. Bhowmik et al., 1995; Sorensen, 1997; Fuehrer and Pagel, 2000; Hüsigg et al., 2000), decrease resuspension of fine sediments (e.g. Brinke et al., 1999;

Rodriguez et al., 2002), and to improve the economical performance of navigation by faster vessels (e.g. Hüsigg and Linke, 1999; Hüsigg et al., 2000). Results and models reported by hydraulic engineers have been widely neglected by biologists and ecologists and *vice versa*. Therefore, although the sustainability principle requires ecological sustainability as well as social and economic sustainability (e.g., Arlinghaus et al., 2002a), hydraulic engineers rarely considered possible effects of navigation-induced physical forces on biological components of the waterways such as fish. Instead, they focused almost exclusively on abiotic components, e.g. erosion and the stability of embankments.

An important missing link between both kinds of scientific disciplines and studies is the swimming performance of fish. The capacity and performance of individual fish to withstand and survive the physical forces, wave actions, and currents during a vessel passage can determine the amount of fish assemblage degradation due to navigation.

Thus, this study reviews the swimming performance of fish with regard to the physical forces mentioned above, in an effort to predict possible impacts of commercial navigation on fish assemblages and fish production in inland waterways. The ecological relevance of fish swimming performance was analysed as a major bottleneck of recruitment in waterways, thus, improving our understanding of the mechanisms structuring fish communities in modified waterways. Ultimately, this study may contribute to conservation and protection efforts of fish communities in waterways to conserve the intrinsic value of fish *per se* (Wolter, 2001b), the ecological services generated by fish (Holmlund and Hammer, 1999), and the fish as self-regenerating natural capital to be used by present and future generations, e.g. by fishing (Arlinghaus et al., 2002a).

The results are prerequisites for a sustainable management approach of waterways in accordance with environmental laws, for example the National Environmental Policy Act of 1969 (NEPA, enacted as P.L. 91-190 on January 01, 1970) in the USA or the European Water Framework Directive (WFD, 2000/60/EEC of December 22, 2000). It is important to mention that NEPA as well as WFD declared national policies to encourage productive and enjoyable harmony between man and environment, and to prevent or eliminate damage to the environment. The recently passed WFD requires the member states to revitalize and to conserve respectively the "good

ecological potential” of the fish community in all artificial and heavily modified water bodies. Therefore, from the sustainable ecosystem management perspective the identification of habitat bottlenecks in waterways should be crucially associated with boat traffic.

This paper starts with a brief literature overview of direct and indirect navigation impacts on fish. Then, the biological orientated literature on swimming performance of fish and the hydraulic engineering orientated aspects of navigation induced physical forces are reviewed. Finally, we will introduce a new concept: the navigation induced habitat bottleneck hypothesis, for short navigation bottleneck hypothesis (NBH). According to this concept, the availability of essential nursery habitats for early life stages of fish is a main limiting factor for fish recruitment and, therefore, a main structuring factor of fish assemblages in waterways. Corresponding to the NBH as introduced here, the swimming performance of juvenile freshwater fish is supposed to be the major recruitment bottleneck resulting from their inability to withstand bank directed navigation induced physical forces.

Effects of navigation on fish

Navigation impacts associated with ship movements can be broadly categorized into direct and indirect stressors. The direct effect is fish mortality caused by the physical forces generated from a moving vessel, such as return currents, shear stress, wash waves and dewatering (Morgan II et al., 1976; Holland, 1986, 1987; Killgore et al., 1987, 2001; Adams et al., 1999b; Odom et al., 1992; Gutreuter et al., 2003). Indirect effects of navigation on fish are vessel induced disturbances preventing fish from nest guarding (Mueller, 1980) or feeding (Barrett et al., 1992), dislodgement of eggs and redistribution of eggs and larvae in less suitable habitats (Hofbauer, 1965; Jude et al., 1998), restricted food availability (Brunke et al., 2002), increasing sediment resuspension and turbidity (Garraff and Hey, 1987; Brookes and Hanbury, 1990; Barrett et al., 1992), and loss of shelter habitats especially macrophytes (Brookes and Hanbury, 1990; Willby and Eaton, 1996).

Direct impacts

Few direct observations are published of fish seriously injured or killed by boat traffic (Rosen and

Hales, 1980; Gutreuter et al., 1999, 2003). From the available experimental or *in situ* investigations of navigation induced physical forces it was concluded, that the direct entrainment of individuals through the propeller zone of passing commercial vessels was the main source of navigation induced fish mortality for eggs, early life stages up to 32 mm total length (Morgan II et al., 1976; Holland, 1986; Killgore et al., 2001), and adults (Gutreuter et al., 2003) due to shear stress created by the towboat propellers. Furthermore eggs and larval fish up to 10–14 days posthatch may become stranded by vessel induced shoreline drawdowns (Holland, 1987; Adams et al., 1999b).

Shear stress

Killgore et al. (2001) evaluated the mortality of ichthyoplankton entrained through a towboat propeller and found a linear relation between shear stress and mortality. Larvae of shovelnose sturgeon (*Scaphirhynchus platyrhynchus*), lake sturgeon (*Acipenser fulvescens*), paddlefish (*Polyodon spathula*), blue sucker (*Cycleptus elongatus*), and common carp (*Cyprinus carpio*) with mean total lengths between 8 mm (blue sucker) and 22 mm (carp) were exposed to four different propeller speeds and the corresponding shear stresses. At the highest shear stress level of 474.3 N m^{-2} , Killgore et al. (2001) reported significantly increased larvae mortalities for all species, ranging between 26.4% in carp and 86% in lake sturgeon. Lake sturgeon as well as blue sucker larvae exhibited significant shear stress mortalities of 21.3% and 74.5% respectively, at the much lower level of 161.3 N m^{-2} (Killgore et al., 2001). Because the upper range of propeller induced shear stress of most towboats at the Mississippi River is 627 N m^{-2} compared to 474.3 N m^{-2} in the experiment, the findings by Killgore et al. (2001) seemed ecologically relevant. In an earlier experiment Killgore et al. (1987) studied the relation between shear stress and duration of turbulence using yolk sac larvae of paddlefish with 14.5–16.1 mm total length range. High shear stress of 632 N m^{-2} resulted in a larval mortality of 86.6% after 10 h for larvae exposed for 30 s once every hour and of 80% after 9 h for larvae exposed once every three hours. Under low shear stress conditions (183.8 N m^{-2}) only 13.3% of the paddlefish larvae died (Killgore et al., 1987). Morgan II et al. (1976) reported for striped bass (*Morone saxatilis*) and white perch (*Morone americana*) egg mortalities at much lower shear stress levels of only 35 N m^{-2} : between 36–38% after one minute, 88% after 4 min and 96% after

10-min exposure. Larvae mortality at the same shear level was found to be 9.3–38% after 1 min, and 68.1–75% after 4 min (Morgan II et al., 1976). Surprisingly, the authors argued, that the experimentally induced shear levels were artificially high and exceeded those along canal shorelines under natural conditions (1.38 N m^{-2}) as well as under navigation conditions (7.89 N m^{-2}), while under laboratory conditions using a true scale barge tow model, Rodriguez et al. (2002) estimated navigation-induced bed shear stress peak values of 100 N m^{-2} (shear velocity 0.3 m s^{-1}) for a duration of about 500 s including bow and stern effects.

In contrast to Morgan II et al. (1976) and Killgore et al. (1987, 2001), no significant differences were found in larvae survival in pre-passage and post-passage samples of loaded barge tows by Holland (1986) and Odom et al. (1992), but Holland (1986) detected significantly increased numbers of damaged eggs (up to 50%) of freshwater drum (*Aplodinotus grunniens*) immediately after loaded tows passed, at shear forces of 9.5 N m^{-2} .

Therefore the resulting “killing volume” (50% of the organisms killed during 1 min exposure) for a typical barge tow was estimated to be 22 m^3 per meter passage (Kennedy et al., 1982, as cited in Holland, 1986). However, the estimated kill area was relatively low compared to typical waterway cross sections (e.g. Hüsiger et al., 2000; Jiang et al., 2002), and propulsion-induced shear forces should generally effect eggs and larvae in the pelagic or mid-channel section of waterways. Therefore, we hypothesized that impacts of shear stress will be of minor importance at the fish assemblage level, because only very few freshwater fish species release their eggs in open waters (pelagophils) or have pelagic eleutheroembryos (litho-pelagophils) (Balon, 1975, 1981).

Dewatering

The effects of dynamic water level changes on fish have been studied in two ways, the exposure to air to simulate dewatering (Holland, 1987) and the stranding potential during drawdowns (Bradford et al., 1995; Bradford, 1997; Adams et al., 1999b; Saltveit et al., 2001).

Eggs and larvae of walleye (*Stizostedion vitreum*) and northern pike (*Esox lucius*) have been experimentally exposed to air for 2 min at 1, 3, 6, or 12-h intervals representing 2–24 tow passages per day (Holland, 1987). A significant mortality due to dewatering events was observed in larvae only. At a dewatering frequency of 3 h, i.e. a simulated passage

of eight commercial tows per day, on average 99% of pike larvae and 49% of the walleye larvae died. The mortality of walleye larvae increased to 59% at a 1-h dewatering frequency simulating 24 tows d^{-1} (Holland, 1987). In an experimental flume with sandy substrate, Adams et al. (1999b) found, that the susceptibility to stranding differed between species, was independent of drawdown rate (cm s^{-1}) and significantly positive correlated with the steepness of the bank slope. For example, a significant species effect was found between both bank slopes used in the experiment: at a slope of 1:5 shovelnose sturgeons of 16.6–18 mm total length had the highest stranding percentage (66.7%) followed by paddlefish (38%), while at a slope of 1:10 blue catfish (*Ictalurus furcatus*) had the highest stranding percentage (26.7%) followed by largemouth bass (*Micropterus salmoides*) with 15.3%. Largemouth bass had a significant higher stranding percentage at a slope of 1:10 than at 1:5, while conversely, the percentage stranded were significantly higher for shovelnose sturgeon, paddlefish, and bluegill (*Lepomis macrochirus*) at a slope of 1:5 than at 1:10 (Adams et al., 1999b). The authors related the probability of stranding to a guild-specific behavioural response to dropping water levels and suggested that mid-channel fish species will be more likely to strand because of their positive rheotaxis, while littoral species swim with the current or drift passively.

In addition to the findings of Adams et al. (1999b), experiments on stranding of juvenile salmonids showed a strong temperature dependence in stranding probability due to lower individual activity at cold temperatures (Bradford et al., 1995; Bradford, 1997; Saltveit et al., 2001), as well as an influence of photoperiod (Saltveit et al., 2001). However, as pointed out by Saltveit et al. (2001), stranding is not equivalent to mortality, as fish were found to survive for several hours in the substrate after dewatering. But in contrast to hydropeaking-induced dewatering (Bradford et al., 1995; Bradford, 1997; Saltveit et al., 2001) the navigation-induced drawdowns last for a maximum of 1–2 min and are followed by a transversal stern wave and a corresponding slope supply current (compare Figures 3 and 4). It seems evident, that a stranding of fish larvae and juveniles due to wash waves is much more likely than due to dewatering.

Indirect impacts

All navigation-induced effects on fish assemblage not directly related to fish mortality are considered to

be indirect effects (reviewed by Liddle and Seorgie, 1980; Murphy et al., 1995), such as the above mentioned vessel-induced disturbances, redistributions and food limitations.

Obstructing nest-guarding behaviour and dislodgement and redistribution of eggs into less suitable habitats lower the reproductive success of various fish species. Male longear sunfish (*Lepomis megalotus*) were found to be driven from their nests by slowly travelling boats and, thus, prevented from nest-guarding which increases the likelihood of egg predation by other fish (Mueller, 1980). In the river Main near the harbour of Würzburg (Germany), Hofbauer (1965) exposed submerged macrophytes with immediately attached eggs of common bream (*Abramis brama*) close to the navigation line and reported 66–96% dislodgment of the eggs after the first day and 75–100% after the second day. Comparable navigation-induced shear velocities up to 0.75 m s^{-1} have been reported by Brunke et al. (2002) from the river Elbe (Germany) on the benthic sediment. The high frictional forces excluded invertebrate taxa living on the sediment surface due to the physical forces, entrainment of sandy sediments, and induced turbidity. Drastically dropping densities of macrocrustaceans and insects (Brunke et al., 2002) can reduce the value of these areas as feeding grounds for fish. As a secondary effect, increased turbidity significantly decreases the reactive distance during feeding, and could, therefore, reduce foraging success. This was experimentally demonstrated using rainbow trout (*Oncorhynchus mykiss*) by Barrett et al. (1992). One of the major indirect impacts on fish resulted from the loss of submerged macrophytes as an ecologically important habitat structure. Macrophyte beds serve as colonizing substrate for various food organisms, as spawning substrate for phytophilic species, and as shelter for juvenile and adult fish. In the British canal system, the increase of recreational boat traffic led to the elimination of fragile macrophyte species as well as to the general decrease of macrophyte biomass (Willby and Eaton, 1996).

However, indirect effects necessarily represent secondary stressors, which can be lowered or manipulated to a certain degree. For example in the regulated river Oder (Germany), juvenile rheophilic fish species were able to inhabit artificial groynes instead of gravel bars lost as a result of hydraulic engineering (Bischoff and Wolter, 2001). Phyto-lithophilic fish prefer submerged macrophytes for spawning, but replace them very easily with roots, woody debris or

other substrates if they have been lost (Balon, 1975, 1981). In contrast to that, the navigation-induced physical forces acting directly on the fish allow only one alternative: to withstand them or not. In this respect swimming performance becomes crucial.

Swimming performance of fish

The swimming performance of fish is characterized by the relation of swimming speed and endurance time, and was classified by Webb (1975a) and Beamish (1978) into three categories: sustained, prolonged, and burst swimming. Sustained swimming is a speed maintained by fish for more than 200 min without fatigue. Prolonged swimming speed can be maintained between 20 s and 200 min and ends in fatigue. Brett (1964) firstly employed a special category of prolonged speed, i.e. the critical speed, as a velocity that a fish could maintain until fatigue for a maximum of 60 min. Burst speed is the highest swimming speed maintained for less than 20 s and is performed anaerobically. A special kind of burst performance is the fast start performance of fish, which represents extremely fast sprints of less than one second duration (e.g. Domenici and Blake, 1997; Reidy et al., 2000), while bursts longer than approximately 2 s will be markedly slower (Hammer, 1995).

Swimming performance depends on a variety of biological and physical factors (Webb, 1975a). Firstly, it is species specific, in a way that body shape (Lindsey, 1978; Webb, 1984a; Wotton, 1990; Vogel, 1994; Walker, 2000; Bergstrom, 2002; Boily and Magnan, 2002), fin form (Webb, 1984a; Videler, 1993; Plaut, 2000), muscle function (Webb and Weihs, 1983; Rome et al., 1988; Altringham and Ellerby, 1999; Kieffer, 2000), and swimming mode (Hertel, 1966; Blake, 1983; Moyle and Cech, 1988; Sfakiotakis et al., 1999; Ellerby et al., 2001; Müller et al., 2001) determine the swimming performance. Secondly, absolute swimming speed increases with fish size (e.g. Blaxter, 1969; Fry and Cox, 1970; Webb, 1976; Beamish, 1978; Hammer, 1995; Domenici, 2001). Thirdly, in ectotherms the swimming performance is temperature dependent (e.g. Brett and Glass, 1973; Beamish, 1974; Otto and O'Hara Rice, 1974; Glova and McInerney, 1977; Wardle, 1980; Fuiman, 1986; Heap and Goldspink, 1986; Keen and Farrell, 1994; Taylor et al., 1996; Wieser and Kaufmann, 1998; Ojanguren and Braña, 2000), although for small fish larvae, viscosity effects are over 10 times more

powerful than the temperature effects not linked to viscosity (see Fuiman and Batty [1997] for an example on herring, *Clupea harengus* of 9.6 mm total length). Fish larvae hatch in a viscous flow regime, and at least in their first week of life, viscosity effects are of considerable importance for the energetic costs of swimming (Blaxter, 1986; Osse and Drost, 1989; Kaufmann, 1990; Müller and Videler, 1996; Wieser and Kaufmann, 1998; Müller et al., 2000). At very low Reynolds numbers (Re = ratio of inertial over viscous forces) of $Re < 10$, viscous forces are paramount and continuous high speed swimming is energetically efficient (Blaxter, 1986). Furthermore, in fish larvae, swimming is almost entirely aerobic up to the highest speeds (Kaufmann, 1990), so that their burst performance is not limited by a restricted anaerobic capacity as in small fish (Kieffer, 2000). Therefore, swimming performance depends also on the ontogenetic stage of a fish (Webb and Weihs, 1986; Hale, 1999). Additional environmental factors influencing the swimming performance of individual fish have been reviewed by Randall and Brauner (1991), Videler (1993), and Hammer (1995), and include pH (Butler et al., 1992; Butler and Day, 1993), oxygen tension (Kaufmann, 1990; Kaufmann and Wieser, 1992; Kieffer, 2000; Reidy et al., 2000), photoperiod (Kolok, 1991), salinity (Randall and Brauner, 1991), and various pollutants (Hammer, 1995).

Ecological relevance of swimming performance

Swimming performance is one of the crucial factors determining the survival of most fish species within the aquatic environment. Predator-prey interactions, reproductive behaviour, especially spawning migrations, habitat shifts and dispersal are of profound ecological importance and depend substantially on the individuals' capacity for locomotion (Kolok, 1999; Reidy et al., 2000). Swimming speed limits and endurance are directly related to food capture, escape from predators and reproduction, and therefore subjected to a strong selection pressure that enhance evolutionary fitness (Beamish, 1978; Videler and Wardle, 1991; Videler, 1993). However, it has not yet been positively proven that critical swimming speed can be directly correlated to Darwinian fitness and survival, but it seems the best ecophysiological measure to predict ecological consequences, especially for riverine fishes that migrate upstream (Plaut, 2001).

Until now, studies and reviews of the ecological relevance of swimming performance focused mainly

on three topics: the above mentioned environmental influences on exercise performance (e.g. Beamish, 1978; Videler, 1993; Hammer, 1995; Kieffer, 2000; Plaut, 2001), migration abilities (Pavlov, 1989; Taylor and Foote, 1991; Barbin and Krueger, 1994; Zerrath, 1996; Toepfer et al., 1999; Ellerby et al., 2001) and predator-prey interactions (Howland, 1974; Webb, 1984b; Fuiman and Magurran, 1994; Domenici and Blake, 1997; van Damme and van Dooren, 1999; Domenici, 2001; Bergstrom, 2002). However, there are substantial differences between the mentioned applications and the ability of fish to withstand short-term physical forces such as return currents during a vessel passage in waterways. On the one hand, the physical stress during a vessel passage is of much shorter duration than fish migration, where, on the other hand, only its maximum speed or absolute performance predicts the individual's survival.

Critical and burst swimming speed of freshwater fishes

Review papers on the different experimental designs to determine fish swimming speeds (Videler and Wardle, 1991; Drueker, 1996; van Damme and van Dooren, 1999; Drueker and Lauder, 2000; Kieffer, 2000; Plaut, 2001) revealed partially contradicting results: van Damme and van Dooren (1999) suggested per unit body length speed as more ecological relevant than absolute speed, while Drueker (1996) found per unit body length speed contributed errors to kinematic and physiological comparisons of exercise between different fishes. Furthermore, studies by Kolok (1999) and Reidy et al. (2000) demonstrated significant variability of locomotor performance between individual fish.

However, to evaluate the swimming performance of fish with regard to the physical forces during vessel passage, absolute values of swimming speeds seem appropriate, because the physical forces are absolute values in terms of drawdown or return current speed. Thus, each individual fish has to withstand a certain threshold value, independent of the kinematic or physiological comparability of its exercise performance (Drueker, 1996). For example, relative swimming performance is negatively correlated with body length (BL), e.g. a 50 cm fish reaches a burst speed of 6 BL s^{-1} , a 5 cm fish of the same species could reach 20 BL s^{-1} . Despite its much better relative performance, a return current of 1.5 m s^{-1} will wash out the small fish (absolute speed 1 m s^{-1}), which the bigger

one can easily withstand using only 50% of its burst performance (absolute speed 3 m s^{-1}).

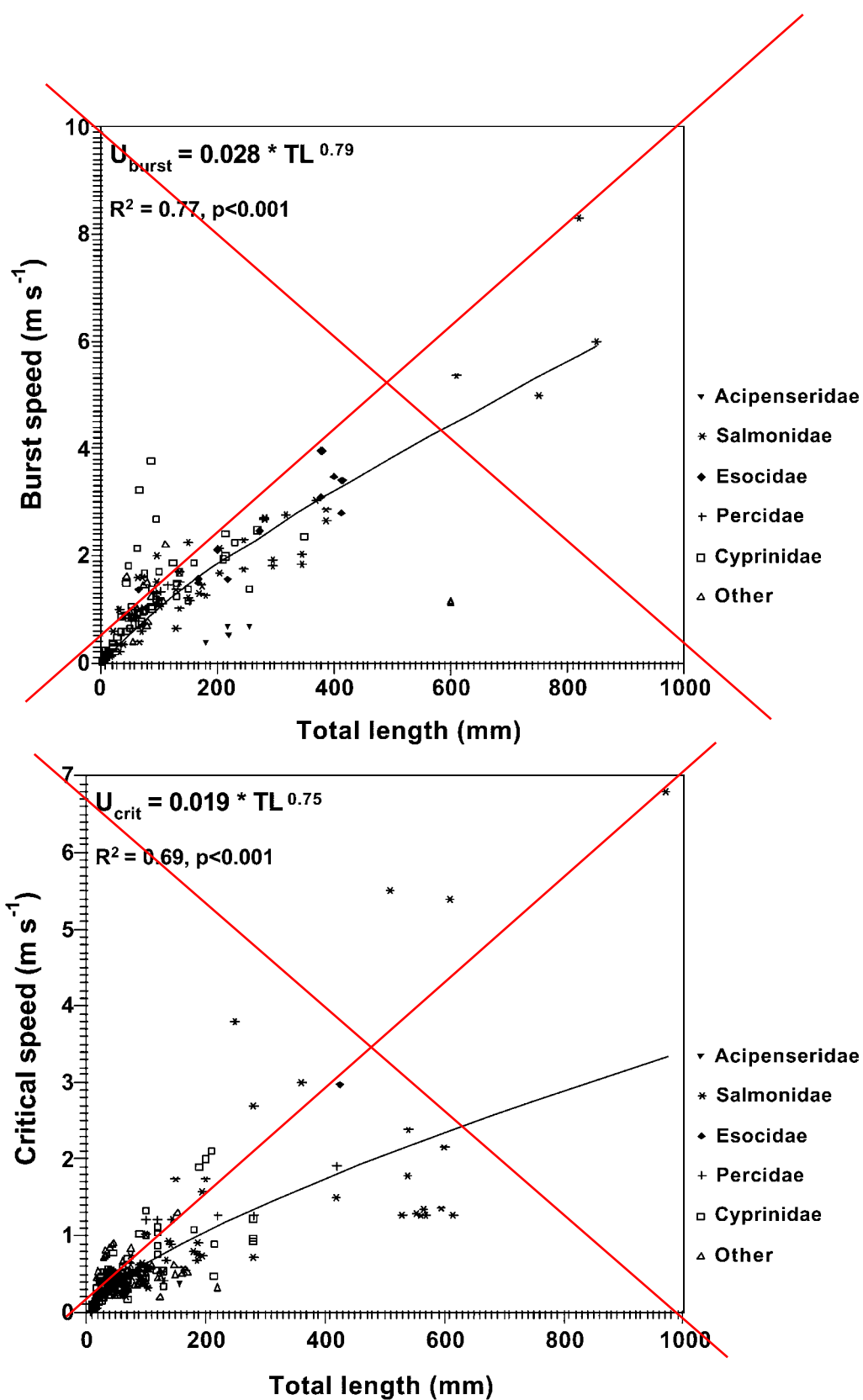
Therefore, the size-dependent absolute swimming speed will be used here to characterize navigation-induced habitat bottlenecks. Despite methodical differences, the available studies of swimming performance of freshwater fish potentially inhabiting or migrating through regulated rivers and waterways (Table 1) were used to compute critical and burst swimming speeds in relation to fish size (Figure 1). In a first step, the data on relative performance have been converted into absolute speeds. After that, fork length and standard length have been converted into total length according to species-specific length-length relations extracted from "Fishbase" (www.fishbase.org). For the general compilation all results have been selected in a temperature range between 10–20°C, because the intraspecific variability of swimming performance reported for different temperatures within this range was comparable among studies (compare e.g. *Oncorhynchus mykiss* in Table 1). A few studies reported only wide temperature ranges (e.g. Jones et al., 1974; Mann and Bass, 1997; Garner, 1999). Altogether eight studies without any indication of experimental temperature (Table 1) were considered to be within this range, mainly because their findings corresponded well with those from similar studies with temperature references. For example, results published by Pavlov (1989) fitted very well with those from an earlier study (Pavlov et al., 1972) for all species in common, such as Russian sturgeon (*Acipenser gueldenstaedtii*), starry sturgeon (*Acipenser stellatus*), stone loach (*Barbatula barbatula*), perch (*Perca fluviatilis*), and roach (*Rutilus rutilus caspius*). Thus, it was reasonable to assume that the swimming speed of the additionally reported species (Pavlov, 1989) were obtained under similar experimental conditions. The same was considered by Blaxter (1969) for the findings reported by Weaver (1963, as cited in Blaxter, 1969) and Radakov (1964, as cited in Blaxter, 1969) ranging around 15°C.

The results selected were separated into two groups: burst performance with a duration $<20 \text{ s}$ and critical performance (up to 1 h). Species were not analysed separately, because most of them were represented by only one or two publications. However, the main families are indicated in Figure 1 suggesting limited differences in swimming performance at small (i.e. potentially imperiled) sizes. A power model fit best and was used for the regression of total length and swimming speed.

Corresponding with the results of a modelling approach used by Haefner and Bowen (2002) to evaluate the functioning of a power plant fish collection gallery, only the absolute burst swimming performance has to be considered as the limiting factor for fish to maintain position successfully in current. Therefore, for larvae and juveniles the burst speed in relation to total length was reanalysed using specimens up to 60 mm total length. All calculations were performed using SPSS software (SPSS Inc., 1999, release 9.0).

The general models of length-specific burst and critical swimming performance were highly significant (Figure 1). As expected, the salmonids exhibited the highest swimming performance in both modes. The wide scattering of results in salmonid critical speeds were mainly related to the wide time scale between 20 s and 1 h (Brett, 1964) for critical performance exercises. The expected outlier in burst performance were eels (*Anguilla anguilla*) and sturgeons with a particularly low burst speed and a few rheophilic cyprinids with a surprisingly high burst speed. The latter findings resulted exclusively from the experiments performed by Zerrath (1996), who reported extremely high burst swimming speeds for small chub (*Leuciscus cephalus*) and gudgeon (*Gobio gobio*) from studies in an experimental fishway. Additional variance of burst speed values was introduced by considering studies of fast-start performance for this compilation, because the maximum speeds held for splits of a second drops substantially after 2–3 s (Hammer, 1995) and declines further within the $<20 \text{ s}$ range of burst performance (Webb, 1975a).

For smaller fish (Figure 2), the general model resulted in the highest available estimation of burst performance for a 50–60 mm long fish. It fits well with Wardle's (1975) calculation of maximum swimming speed on the basis of white lateral muscle's contraction time and the relation between tailbeat frequency and forward motion (Figure 2). The correspondence of the model is satisfactory as well with the results for common carp by Wakeling et al. (1999), for the rheophilic nose carp (*Chondrostoma nasus*) by Flore et al. (2001), and for roach (*Rutilus rutilus*) and dace (*Leuciscus leuciscus*) by Garner (1999). However, the mean burst speed calculated represents the uppermost limit for most of the common eurytopic species due to the strong swimmers considered like salmonids or rheophilic cyprinids (Figure 2), and, thus, a conservative estimation of possible navigation impacts.



~~Figure 1. General models of burst speed and critical speed of freshwater fish compiled from various studies (for references compare Table 1).~~

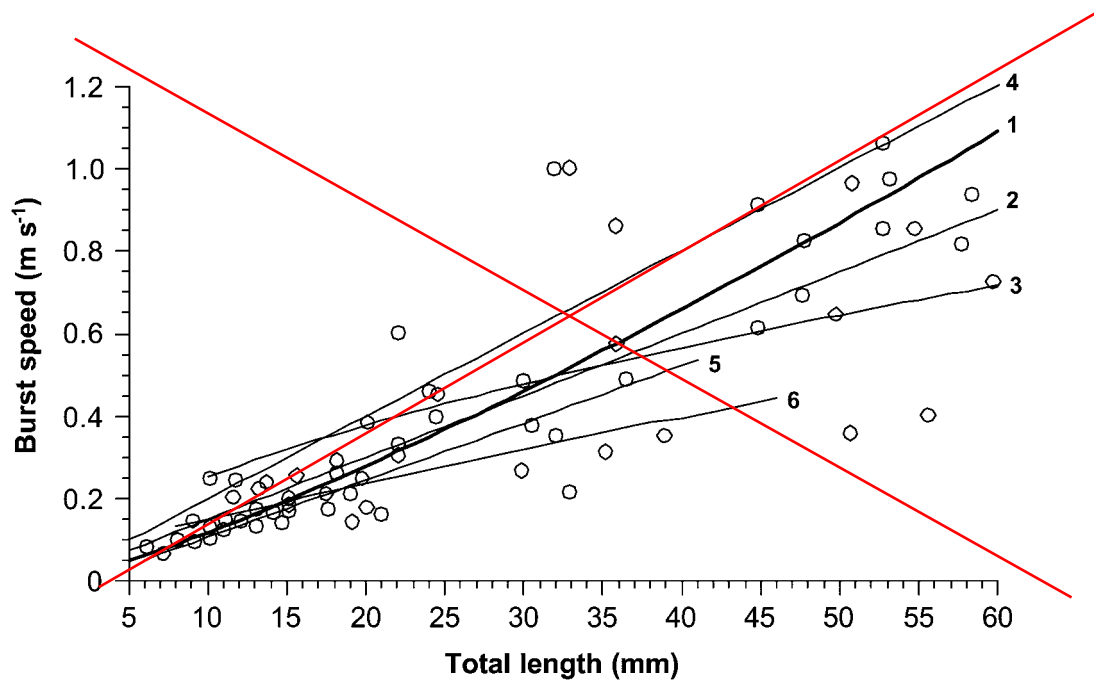


Figure 2. Size-dependent burst performance of small fish up to 60 mm total length compiled from Table 1. Numbers refer to burst speeds according to (1) own model $U_{burst} = 0.0068 \cdot TL^{1.24}$, $R^2 = 0.83$, $p < 0.001$; (2) Wardle (1975); (3) Wakeling et al. (1999) for carp; (4) Flore et al. (2001) for nose carp; and Garner (1999) for (5) roach, and (6) dace.

To better evaluate the potential impacts of navigation-induced forces such as wash waves on fish, the next section briefly describes navigation-induced physical forces.

Navigation-induced physical forces

Inland waterways are restricted in depth and often in width. Barge traffic in a restricted waterway is associated with significant temporary changes of the aquatic environment. The size of the vessel with respect to the waterway along with its speed dictates the magnitude of these changes. The movement of a solid body (vessel's hull) through the water (Figure 3) displaces water and creates a wave in front resulting in increasing hydraulic pressure at the bow (Bhowmik and Mazumder, 1990; Sorensen, 1997; Oebius, 2000b). Directly related to its increase in front of the vessel, the water level drops along the vessel's hull resulting in drawdown and a return velocity opposite to the moving direction (Figure 3). Drawdown begins near the bow and rebounds near the stern producing a single wave with a duration depending on vessel length. Drawdown causes dewatering of shallow areas along the shoreline during vessel passage (Bhowmik and Mazumder, 1990; Soong and Bhowmik, 1992;

Sorensen, 1997; Oebius, 2000b; Stockstill and Berger, 2001). The magnitude of the pressure gradient and the total pressure change strongly depend on the ratio of ship cross section A_s determined by maximum width and draught of a tow, and wetted canal cross section A_c , i.e. on the clearance between vessel's hull and channel side and bottom, which determines the hydraulic pressure necessary for the displaced water to pass the moving vessel and, thus, the height of the front wave (Oebius, 2000b). When responding to sharp pressure gradients at the bow and at the stern, which induce the rapid rise and fall in water surface (drawdown), inertia causes the water surface to lag behind its equilibrium position and produces a surface oscillation. This, in turn, produces the wave patterns that propagate out from the vessel (Bhowmik et al., 1992, 1995; Mazumder et al., 1993; Sorensen, 1997). Consequently, the displacement forces also depend on the relative velocity of the flow past the hull and thus, on the speed of the vessel (Bhowmik and Mazumder, 1990; Sorensen, 1997; Hüsiger and Linke, 1999; Oebius, 2000b; Jiang et al., 2002). The conversion of pressure into kinetic energy results in increasing return velocities directly related to the height of the front wave (Oebius, 2000b). With decreasing $A_c:A_s$ ratio, the front wave as well as the return current will increase and, therefore, also

the dynamic water level sinkage (squat or drawdown) alongside the ship (Bhowmik and Mazumder, 1990; Maynard and Siemsen, 1991; Sorensen, 1997). Corresponding with raising return currents both the slope supply current and the transversal stern wave will raise up (Figure 3). The velocity structure is composed of two parts, the barge-induced displacement velocities mentioned above (return current, slope supply current) and the towboat-induced propeller jet velocities. Propeller jet effects like shear stress are limited to the area behind the tow in the navigation lane (Bhowmik and Mazumder, 1990; Mazumder et al., 1993; Fuehrer, 1998; Linke et al., 2002).

Navigational speeds on depth-restricted waters are typically characterized according to the depth-related Froude number (F_d) giving the relation between vessel speed (V) and the velocity of a progressive wave. Displacement forces reach their maximum at critical vessel speeds (V_{crit}), when the vessel speed equals the speed of the front wave (Oebius, 2000b), characterized by Froude numbers ranging between $0.8 < F_d < 1.1$ (Hüsig and Linke, 1999; Hüsig et al., 2000). Operating at speeds resulting in $F_d < 1$ is defined as subcritical and $F_d > 1$ as supercritical (Hüsig et al., 2000). While in deep unrestricted waters fast ships commonly operate in the supercritical mode, in inland waterways all conventional ships operate generally in the subcritical mode (Hüsig and Linke, 1999; Hüsig et al., 2000). In restricted inland waterways, most of the commercial displacer vessels operate at $F_d = 0.5$ – 0.6 and fast inland vessels at $F_d = 0.7$ – 0.9 (Abdel-Maksoud and Heinke, 2002).

Field and laboratory studies of navigation effects on embankment structures reported bow waves of 0.20 – 0.82 m height (Jähne et al., 1993; Maynard, 1999; Fuehrer and Pagel, 2000), drawdowns between 0.10 – 0.95 m (Soong and Bhowmik, 1992; Jähne et al., 1993; Maynard and Martin, 1997; Fuehrer, 1998; Maynard, 1999; Fuehrer and Pagel, 2000; Heibaum and Soyeaux, 2002), return currents between 0.4 – 1.1 m s^{-1} (Maynard and Martin, 1997; Fuehrer, 1998; Maynard, 1999, 2000; Heibaum and Soyeaux, 2002) at subcritical tow speeds, and 1.2 – 1.7 m s^{-1} at critical tow speeds (Fuehrer, 1998; Fuehrer and Pagel, 2000; Oebius, 2000b), and transversal stern (wash) waves along the shore up to 0.7 m height (Heibaum and Soyeaux, 2002). Thus, in German waterways for example, the working guidelines for hydraulic engineering demand the construction of embankments designed for drawdowns of 0.6 m and bank-directed currents of 2 m s^{-1} (Fuehrer, 1998).

Because the largest changes take place in a zone within 10% of the channel width from shore (Mazumder et al., 1993), these navigation-induced physical forces represent significant disturbances for littoral communities of aquatic organisms. Apart from their magnitude, duration and frequency of these disturbances are especially important. For example, Bauer et al. (2002) estimated bank erosion of 0.01 – 0.22 mm sediment per boat passage.

The main physical impacts during a vessel's passage last generally between 10 – 60 s (Figure 4; Bhowmik et al., 1995; Oebius, 2000b; Heibaum and Soyeaux, 2002), in maximum up to 2 – 3 min depending on the total length of the vessel (Holland, 1986, 1987; Nielsen et al., 1986; Bhowmik and Mazumder, 1990; Jähne et al., 1993; Hüsig et al., 2000; Oebius, 2000b; Arlinghaus et al., 2002b; Brunke et al., 2002). However, Rodriguez et al. (2002) reported maximum values of more than 8 min (500 s) including bow and stern effects.

The frequency of disturbances was estimated from waterway statistics of lock operations and passages of commercial tows (e.g. WSD Ost, 2002; Summaries of U.S. lock statistics at www.iwr.usace.army.mil/ndc/publications.htm, and of German inland navigation statistics at www.elwis.de/Verkehrsstatistik). The ship counts varied dramatically between waterways. While in less frequented waterways around 200 commercial tows per year have been counted in 2001 (e.g. Tennessee Tombigbee Waterway in the USA), their number was more than 150 -fold higher at navigation hotspots (e.g. $30,801$ in the German Rhine at Iffezheim in 2001). In North American and European waterways typical frequencies of commercial tow passages ranged between $1,000$ – $6,000$ per year; however, more than $10,000$ per year were not rare. This means an average daily disturbance of 0.6 – 84 commercial vessel passages, commonly between 2.7 – 16.4 vessels per day. Thus, according to their frequency, navigation-induced disturbances differ significantly from comparable hydraulic impacts from hydropower stations. Although especially propeller-typed turbines of power-generating facilities impact fish similar to navigation by shear forces, pressure changes, and strong currents (Cada, 1990; Hadderingh and Bakker, 1998; Turnpenny, 1998; Gutreuter et al., 1999, 2003; Haefner and Bowen, 2002), there is a significant difference between both stressors in the spatial dimension too. While hydraulic forces induced by power-generation act locally and influence mainly drifting or migrating fish, those from a moving vessel act along

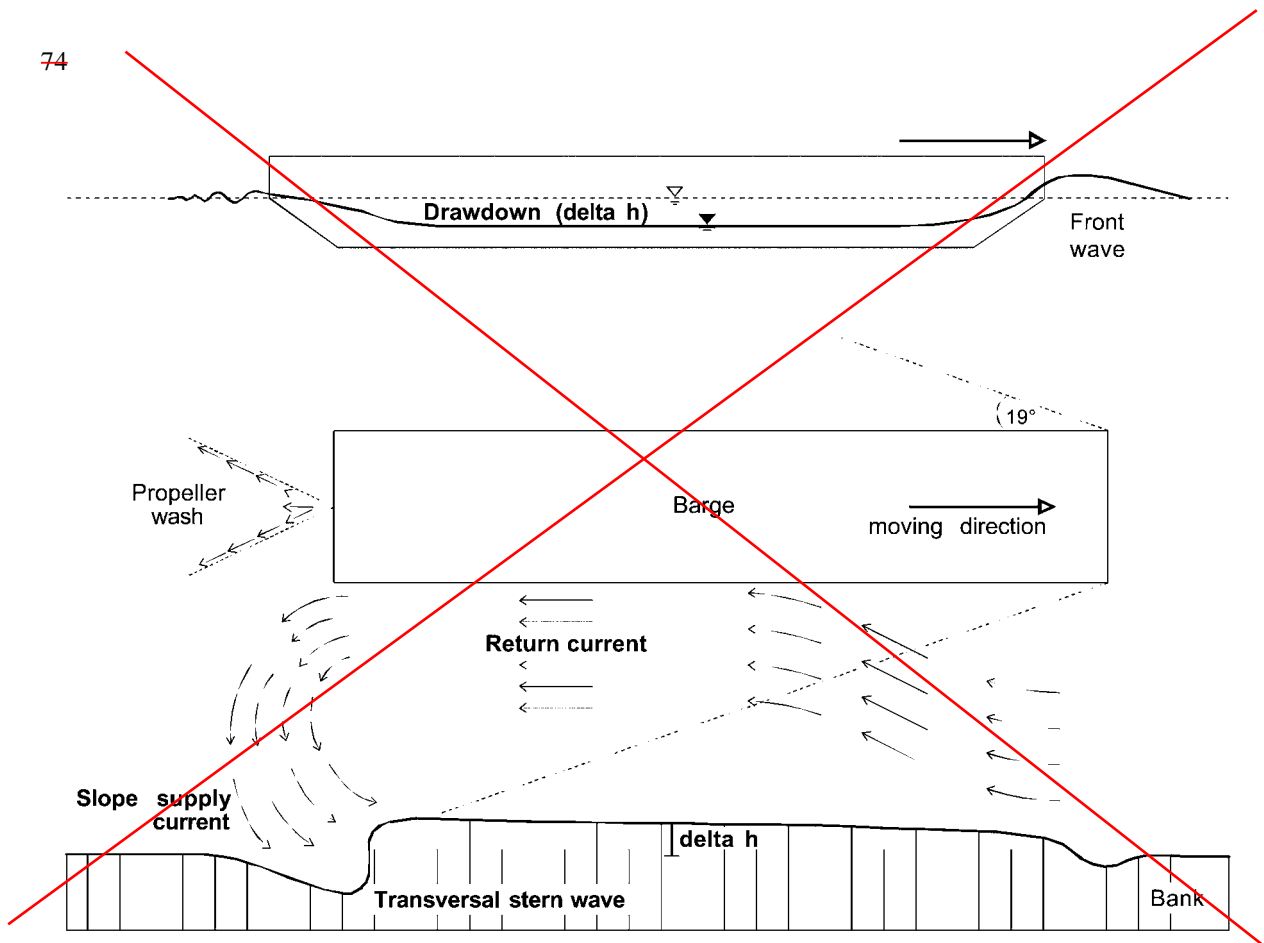


Figure 3. Navigation-induced physical forces in restricted waterways (modified from Bhowmik and Mazumder, 1990; Fuehrer, 1998; Oebius, 2000b).

the complete navigable waterway and potentially influence all fish therein. This means, fish are generally unable to avoid navigation-induced hydraulic forces in the navigation mainchannel.

Standard cargo vessels at European waterways are allowed to navigate 10 km h^{-1} for full draught and 12 km h^{-1} for unloaded vessels (Hüsiger et al., 2000). At a typical ratio between wetted canal cross section A_c and the cross section of the standard vessel of $A_c:A_s = 5.5$ the resulting Froude number ranges between $0.44 < F_d < 0.53$ (Hüsiger et al., 2000) which is well within the subcritical mode (Fuehrer, 1998; Hüsiger and Linke, 1999; Fuehrer and Pagel, 2000; Hüsiger et al., 2000; Maynard, 2000; Oebius, 2000b; Jiang et al., 2002). According to our own measurements in a representative navigation canal in the German lowlands, at a ratio $A_s:A_c = 0.14$ (corresponding to $A_c:A_s = 7.4$) and vessel speeds of $80\text{--}90\% V_{crit}$, the navigation-induced return currents along the shore were usually around 0.8 m s^{-1} accompanied by a $0.1\text{--}0.3 \text{ m}$ drawdown (compare Figure 4). Although this hydraulic force is

well below the critical mode ($F_d \approx 1$, representing the highest hydraulic pressure), it is in the range of burst performance (withstand less than 20 s) for fish of $<47 \text{ mm}$ total length (Figure 2) and of critical performance ($>20 \text{ s}$ to 1 h without fatigue) for fish $<147 \text{ mm}$ (Figure 1) and should, therefore, influence survival and recruitment of fish in waterways. This led to the formulation of the navigation-induced habitat bottleneck hypothesis (NBH), which will be introduced below.

Navigation-induced habitat bottleneck hypothesis (NBH)

According to the NBH concept, fish recruitment is limited because of a lack or restricted availability of essential nursery habitats resulting from navigation-induced hydraulic forces that exceed the maximum swimming performance of fish.

Nearly all fish larvae, except pelagophils and litho-pelagophils, have their first nursery habitats in

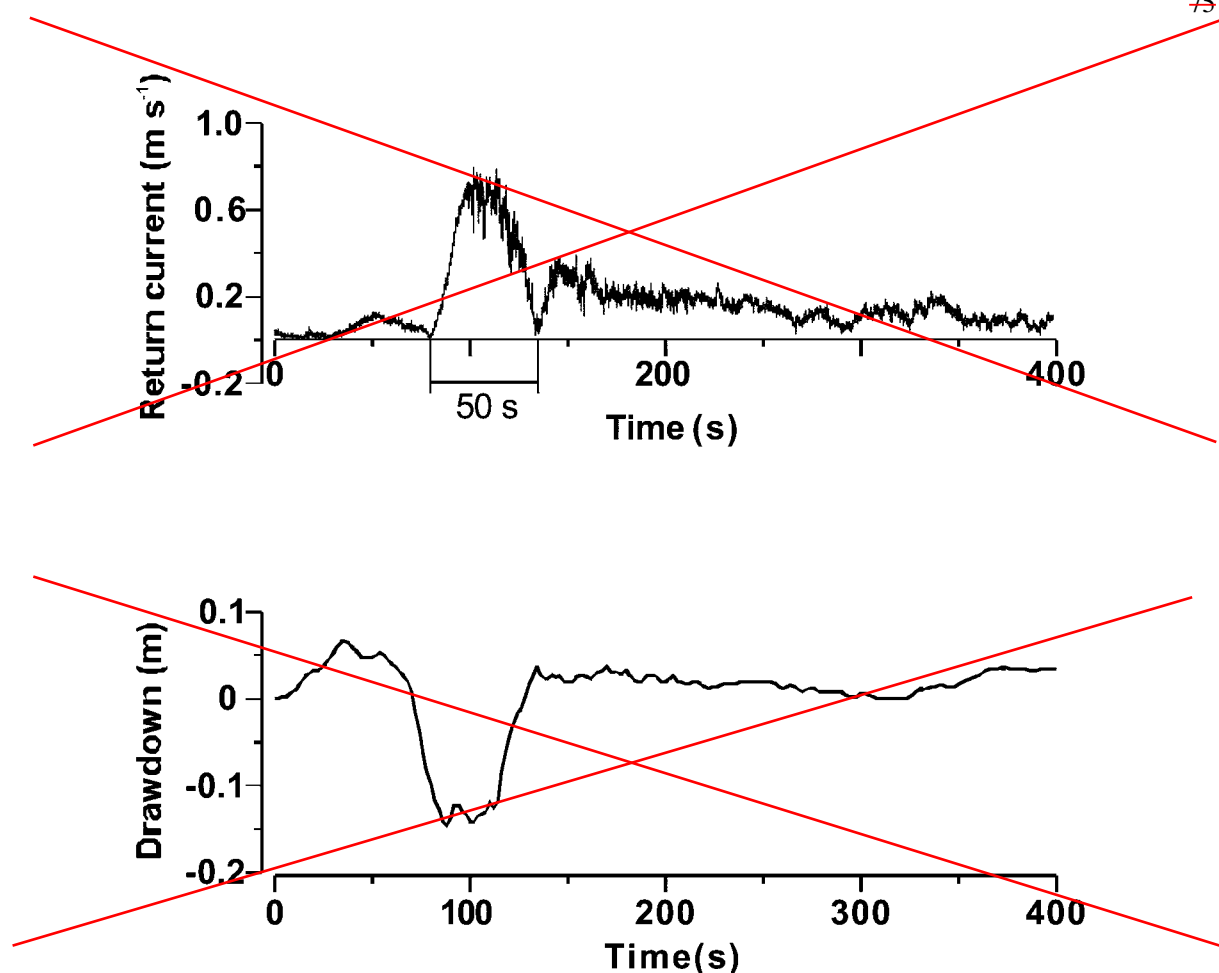


Figure 4. Typical return current patterns and dynamic water level sinkage measured during the passage of a 81.5 m barge tow at 8.0 km h^{-1} and an A_y/A_r ratio of 0.14 in a German waterway (data source Arlinghaus et al., 2002b).

shallow, low flowing, littoral areas (e.g. Schlosser, 1985; Copp, 1989; Scheidegger and Bain, 1995; Staas, 1997; Cowx and Welcomme, 1998; Gaudin, 2001; Grift, 2001; Schiemer et al., 2001; Bischoff, 2002). In these areas, especially in the upper half of the bank slope (Fuehrer, 1998), the commercial navigation traffic generates the maximum hydraulic impact (Mazumder et al., 1993; Daemrich et al., 1996; ASCE Task Committee, 1998; Fuehrer, 1998; Fuehrer and Pagel, 2000; Thornton et al., 2000), mainly due to the amplitude of the transversal stern wave (Sorensen, 1997; Fuehrer, 1998; Bauer et al., 2002) and the speed of the slope supply current (Bhowmik and Mazumder, 1990; Bhowmik et al., 1995; Oebius, 2000b; Jiang et al., 2002; Rodriguez et al., 2002). Freshwater fish larvae hatch at total length of 2.7–9.5 mm and swim free between 6–15 mm (Koblickaya, 1981; Pinder,

2001). Up to a total length of 20 mm, their mean burst performance will range between 0.06 – 0.19 m s^{-1} (for 6–15 mm fish) and not exceed 0.28 m s^{-1} (Figure 2). However, the navigation-induced currents measured in their preferred habitats ranged between 0.75 – 0.8 m s^{-1} (Brunke et al., 2002; Figure 4) and more than 1 m s^{-1} (e.g. ASCE Task Committee, 1998; Fuehrer and Pagel, 2000; Maynard, 2000; Oebius, 2000b; Jiang et al., 2002; Rodriguez et al., 2002). Thus, the strongest trade-off exists between the poor swimming performance of small fish larvae and the wash waves or backwash currents close to the shore.

In contrast to the above mentioned studies of direct and indirect navigation impacts on fish, the real bottleneck for larvae survival will be created by the transversal slope supply currents directed to the bank (Figure 3). This may force many fish species

through a navigation-induced habitat bottleneck in waterways, when they are unable to survive in their essential habitats due to their restricted swimming performance. According to this navigation-induced habitat bottleneck hypothesis (NBH), ship traffic may be a major force structuring fish communities in waterways.

Primary stressors

As it was shown in Figure 1, for any fish larger than 200 mm total length no direct effects due to navigation-induced currents are expected. Their critical performance is around 1 m s^{-1} , and their burst performance corresponds with the basis of assessment of maximum hydraulic pressure for embankment stability of 2 m s^{-1} (Fuehrer, 1998). In contrast to that, a critical bottleneck for fish survival must be expected in the lower length groups at the highest flow velocities.

For the prediction of possible navigation impacts on fish the burst performance respectively the maximum critical performance will be used, because main physical impacts during a vessel's passage last generally between 10–60 s, in maximum up to 2–3 min depending on the total length of the vessel (Figure 4; Holland, 1986, 1987; Bhowmik and Mazumder, 1990; Hüsig et al., 2000; Oebius, 2000b; Arlinghaus et al., 2002b; Brunke et al., 2002; Rodriguez et al., 2002). As was illustrated above (Figures 1 and 2), swimming performance is a function of size. A small fish of 40 mm total length reaches a burst swimming speed between 0.6 – 0.8 m s^{-1} (Figure 2) and a critical swimming speed of about 0.3 m s^{-1} (Figure 1). The burst swimming speeds are within the range of return and transversal currents reported from studies on navigation effects on embankment structures: commonly peaking $>0.7 \text{ m s}^{-1}$ (e.g. Fuehrer, 1998; Maynard, 2000; Oebius, 2000b). According to these studies, at the allowed (Hüsig et al., 2000) subcritical vessel speeds ($F_d < 0.5$) navigation-induced currents of 0.6 – 1.0 m s^{-1} close to the shoreline are usual and common. This limits the availability of shoreline habitats for fish with a lower absolute swimming performance than 0.6 m s^{-1} . It is especially a limitation for small fish <40 mm total length in general (Figure 2) and fish larvae in particular who depend on shallow sheltered shoreline habitats as nursing ground. They are too small and weak to withstand the navigation-induced waves and currents and will become washed out. It is not necessarily the case that all larvae once

washed out die. They may also be washed into the waterway again, in particular during dense traffic times. However, damages at artificial embankments such as rip raps are very likely. Furthermore, terrestrial insects prey on larvae washed outshore (M. Brunke, personal communication). Therefore, high mortality is very likely.

Secondary stressors

The danger to become washed out decreases with an increasing distance from shore, but in rivers, the food availability for small larvae decreases as well offshore, because of a general decreasing zooplankton abundance in turbulent waters (e.g. Bohle, 1995). Therefore secondary stressors could become increasingly important. Navigation-induced wave stress prevents fish larvae from feeding and thus restricts their swimming performance, because absolute U_{crit} will decline at lower ration levels (Beamish et al., 1989; Gregory and Wood, 1999). For example juvenile rainbow trouts fed with rations of 0.5% biomass day^{-1} showed the poorest relative ($BL \text{ s}^{-1}$) and absolute (cm s^{-1}) swimming performance compared with parallel groups fed with 1 – 2% biomass day^{-1} (Gregory and Wood, 1999). Similar findings have been reported by Beamish et al. (1989): After 70 days of feeding a significantly positive correlation was found between carcass protein content and critical swimming speed in juvenile lake trout (*Salvelinus namaycush*). In juvenile rainbow trout fasting for 4–5 days can cause significant reductions in white muscle glycogen stores, one of the three endogenous fuels for burst activity, while the other two, ATP and phosphocreatine remain conserved during food deprivation (Kieffer and Tufts, 1998). Burst exercise is largely supported by anaerobic glycolysis within the white muscle (reviewed in Kieffer, 2000). Decreased glycogen levels ultimately limit the anaerobic capacity of fish, and therefore, fasted fish display a lower burst performance compared to fed fish.

Similar results have been obtained from studies of fish passage through hydropower turbines (reviewed by Coutant and Whitney, 2000). Intake-specific turbulence and vortices act in the same way as navigation-induced: disorientation of small fish and little behavioral control during passage, and thus, increasing stress and preventing from feeding for a while.

Ultimately, higher energy cost for swimming, reduced food intake and reduced swimming performance as a result of navigation can result in higher

mortality through predators because the time to reach the size-refuge will be enlarged.

Empirical evidence

There are at least two empirical indications derived from studies on fish assemblages in waterways that support the NBH presented here. Firstly, it was proposed that navigation impacts may lead to a shift of fish community composition (Linfield, 1985; Pygott et al., 1990). Evidence for this pattern was given by Wolter and Vileinskas (1997). In European rivers, perch (*Perca fluviatilis*) rarely reaches relative abundances $>10\%$, however, in heavily modified German waterways the relative abundance of perch typically increased to 30–50% (Wolter and Vileinskas, 1997). This may be the result of two mechanisms: (a) the ontogenetic niche shift of perch larvae from the littoral to the pelagial resulting in lower exposure to the transversal slope supply current and lower associated mortality, and (b) the comparably higher mortality of many other larvae of different species bound to the shore and directly exposed to the slope supply current (Wolter and Vileinskas, 1997; Arlinghaus et al., 2002b). This pattern might favour perch over other species such as roach under anthropogenic influences in waterways, which has led to the suggestion of “perch as an indicator species for structural degradation in regulated rivers and canals” (Wolter and Vileinskas, 1997).

Secondly, Arlinghaus et al. (2002b) studied the fish recruitment in a navigable canal the Oder-Havel-Kanal (OHK) in the German lowlands. In the OHK even among (loose) vegetation, the slope supply current reached velocities up to 0.2 m s^{-1} in bays and 0.8 m s^{-1} in straight reaches, at the burst performance of fish larvae and juvenile fish ranging between 15–47 mm respectively. Therefore, in the OHK, a high larvae mortality as a result of shipping was conceivable, most likely in the straight reaches. The observed fish distribution (Arlinghaus et al., 2002b) corresponded very well with the predicted limitations resulting from swimming performance. The juvenile fish started to colonize the straightened canal stretches when reaching a mean total length of 45 mm in July, and spread therein in August with total length of 50–70 mm. With increasing body length, fish were apparently able to colonize the straight reaches with less risk of being washed out by ship waves (Arlinghaus et al., 2002b). Similar findings have been reported from English rivers by Lightfoot and Jones (1996)

and Duncan et al. (2001). Fish preferred microhabitats in the river with very low flows, which could be maintained at sustained swimming performance. With increasing body length fish were found to cruise at higher swimming speeds (Lightfoot and Jones, 1996) and to utilize faster flowing habitats (Duncan et al., 2001). Colonization of straight reaches of the OHK occurred first when juvenile fish had reached 35 mm total length (Arlinghaus et al., 2002b). This represents the lower limit of threshold range of burst performance ($0.6\text{--}0.8 \text{ m s}^{-1}$) derived from the NBH.

Conclusion

In addition to the navigation-related impacts, such as dredging, rectification and artificial embankments in waterways, many direct and indirect impacts on fish are conceivable resulting from physical forces associated with shipping. The most pronounced may be related to high fish larvae mortality due to bank-directed slope supply currents. Although in waterways the allowed vessel speeds of 10 km h^{-1} (full draught barge) respectively 12 km h^{-1} (empty barge) of typical cargo ships or pushing tows are generally well in the subcritical mode between $0.44 < F_d < 0.53$ (Hüsig et al., 2000), the resulting navigation-induced return and slope supply currents significantly exceed the swimming performance of larvae and small fish. According to the NBH, small fish up to approximately 40 mm total length are unable to withstand the vessel generated currents of $0.6\text{--}1 \text{ m s}^{-1}$ for more than a few seconds. Inshore structures such as macrophytes, stones or woody debris may reduce this total length threshold, as the generated currents predicted from hydraulic models may be lowered in structured microhabitats (Sand-Jensen and Pedersen, 1999). Pearsons et al. (1992) stressed the role of habitat complexity with respect to the extent of wash-out effects due to floods which are comparably to navigation-induced increase of flow velocity. Increasing habitat complexity provides more refuges with lower flows. In contrast to the experimental setup to measure swimming performance (reviewed in Drucker, 1996; Kieffer, 2000), under natural conditions the flow patterns are much more variable. With increasing roughness of the substrate the velocity gradient becomes spread and the flow velocities close to the bottom lowered (e.g. Fuehrer, 1998; Maynard, 1999; Oebius, 2000b). However, considering the duration of a typical wave pattern of at least 40–50 s (compare Figure 4) and the size

and swimming ability of fish larvae (Figure 2), these navigation-induced physical forces certainly limit fish reproduction in waterways and are therefore major environmental forces structuring fish communities in waterways. Under those navigation conditions fish reproduction is restricted to areas more distant to the mid-channel and to the shipping line, e.g. bays (Arlinghaus et al., 2002b) or backwaters (Staas, 1997; Gaudin, 2001; Schiemer et al., 2001), respectively to stretches with higher structural diversity (e.g. Pearsons et al., 1992; Sand-Jensen and Pedersen, 1999).

Further modelling studies and field investigations should be performed to test the NBH predictions. Hydraulic modelling of navigation-induced physical forces is a prerequisite to link hydraulic and biological models to predict shipping-induced mortalities of the species present in waterways. However, *in situ* it is very difficult to distinguish navigation-induced fish mortality from other anthropogenic causes as well as from natural mortality. Experiments should be designed at structurally and ecologically similar sites where shipping influences can either be excluded or omitted to allow a comparable sampling at reference sites without navigation impacts. Furthermore, long-term studies before and after the planned enhancement of inland navigation could provide a verification of the NBH by detecting fish assemblage shifts directly related to increased navigation.

Prospect for the future

Plans to improve the capacity of inland waterways and vessels (Bartell and Campbell, 2000; European Commission, 2001) will intensify this navigation-induced bottleneck in the life history of fishes in two ways. Firstly, improvement of waterways always means rectification, enlargement and regulation, and thus bays, backwaters and tributaries will be lost or separated from the main channel, and a higher percentage of the shoreline area will be effected by the mentioned hydraulic forces. Drawdown, return current, transversal stern wave, and slope supply current are strongly negative correlated with the distance of the vessel from the shore (Arlinghaus et al., 2002b). The hydraulic pressure increases exponentially if the barges move closer to the bank (outside the middle of the channel) which has to be expected will increase when more vessels pass each other (Fuehrer, 1998; Fuehrer and Pagel, 2000; Maynard, 2000; Oebius, 2000b; Jiang et al., 2002). Secondly, improve-

ment of vessel's capacity focus on the use of bigger, more efficient vessels. Increasing draught or width will increase the ships cross section A_s and therefore also the $A_s:A_c$ ratio which is directly related to raising hydraulic forces and F_d values.

To sum up, in its present form the improvement of commercial navigation traffic will substantially impact the fish assemblages in waterways and cause a considerable decline of species diversity as well as fish production due to limited reproduction resulting from a bottleneck in larvae survival. The latter results from their limited swimming performance in regard with navigation-induced hydraulic forces. However, this strong dependence opens up possibilities of formulating suitable criteria for safe ship operation (speed and distance to bank) as well as for effective fairway management (construction and maintenance) and sustainable fish conservation (species recruitment and production). Conserving the "good ecological potential" of fish communities in waterways according to the WFD (2000/60/EEC) or its sustainable management in accordance with NEPA requires minimizing of navigation impacts, for example by enhancing shoreline structures, ecotone diversity and enlargement or by revitalizing submerged and emerged macrophytes (e.g. Arlinghaus et al., 2002b; Wolter, 2001b).

In further construction works in waterways, it is advisable to preserve existing bays and tributaries and even create additional ones. Furthermore, it is recommended to structure the banks as a mosaic with varying stretches of sheet pile wall (where necessary), rip rap, allochthonous gravel and more natural shorelines. This more ecologically orientated engineering will not severely constrain commercial navigation and their socioeconomic benefits, but it will substantially enhance fish recruitment in waterways and their ecological sustainability for the overall benefits of fish, fisheries and society. Considering the NBH, the most environmentally sound mode of transport in regard to greenhouse gas emissions could be improved to be sustainable as well in regard to maintain aquatic organisms.

Acknowledgements

We thank Dr. Jennifer Nielsen and two anonymous reviewers for comments and suggestions that substantially improved the manuscript.

References

- Abdel-Maksoud, M. and Heinke, C. (2002) Fast ships — Hydrodynamic modeling and economic aspects. *Mitteilungen aus dem Franzius-Institut für Wasserbau und Küsteningenieurwesen* **88**, 90–98.
- Adams, C.E. (1993) Environmentally sensitive predictors of boat traffic loading on inland waterways. *Leisure Studies* **12**, 71–79.
- Adams, S.R., Hoover, J.J. and Killgore, K.J. (1999a) Swimming endurance of juvenile pallid sturgeon, *Scaphirhynchus albus*. *Copeia* **1999**, 3, 802–807.
- Adams, S.R., Keevin, T.M., Killgore, K.J. and Hoover, J.J. (1999b) Stranding potential of young fishes subjected to simulated vessel-induced drawdown. *Trans. Am. Fish. Soc.* **128**, 1230–1234.
- Altringham, J.D. and Ellerby, D.J. (1999) Fish swimming: patterns in muscle function. *J. Exp. Biol.* **202**, 3397–3403.
- Arlinghaus, R., Mehner, T. and Cowx, I.G. (2002a) Reconciling traditional inland fisheries management and sustainability in industrialized countries, with emphasis on Europe. *Fish and Fisheries* **3**, 261–316.
- Arlinghaus, R., Engelhardt, C., Sukhodolov, A. and Wolter, C. (2002b) Fish recruitment in a canal with intensive navigation: implications for ecosystem management. *J. Fish Biol.* **61**, 1386–1402.
- ASCE Task Committee on Hydraulics, Bank Mechanics, and Modelling of River Width Adjustment (1998) River width adjustment. I: Processes and mechanisms. *J. Hydraul. Eng.* **124**, 881–902.
- Bainbridge, R. (1960) Speed and stamina in three fish. *J. Exp. Biol.* **37**, 129–153.
- Balon, E.K. (1975) Reproductive guilds of fishes: a proposal and definition. *J. Fish. Res. Board Can.* **32**, 821–864.
- Balon, E.K. (1981) Additions and amendments to the classification of reproductive styles in fishes. *Env. Biol. Fish.* **6**, 377–389.
- Barbin, G.P. and Krueger, W.H. (1994) Behaviour and swimming performance of elvers of the American eel, *Anguilla rostrata*, in an experimental flume. *J. Fish Biol.* **45**, 111–121.
- Barrett, J.C., Grossman, G.D. and Rosenfeld, J. (1992) Turbidity-induced changes in reactive distance of rainbow trout. *Trans. Am. Fish. Soc.* **121**, 437–443.
- Bartell, S.M. and Campbell, K.R. (2000) *Ecological Risk Assessment of the Effects of the Incremental Increase of Commercial Navigation Traffic (25, 50, 75, and 100 Percent Increase of 1992 Baseline Traffic) on Fish*. U.S. Army Corps of Engineers, Upper Mississippi River — Illinois Waterway System Navigation Study, ENV Report 16. 132 pp.
- Bauer, B.O., Lorang, M.S. and Sherman, D.J. (2002) Estimating boat wake induced levee erosion using sediment suspension measurements. *J. Waterway, Port, Coastal, Ocean Eng.* **128**, 152–162.
- Beamish, F.W.H. (1974) Swimming performance of adult sea lamprey, *Petromyzon marinus*, in relation to weight and temperature. *Trans. Am. Fish. Soc.* **115**, 143–148.
- Beamish, F.W.H. (1978) Swimming capacity. In: Hoar, W.S. and Randall, D.J. (eds.), *Fish Physiology. Vol. VII—Locomotion*. Academic Press, New York, pp. 101–187.
- Beamish, F.W.H., Howlett, J.C. and Medland, T.E. (1989) Impact of diet on metabolism and swimming performance in juvenile lake trout, *Salvelinus namaycush*. *Can. J. Fish. Aquat. Sci.* **46**, 384–388.
- Bergstrom, C.A. (2002) Fast start swimming performance and reduction in lateral plate number in threespine stickleback. *Can. J. Zool.* **80**, 207–213.
- Bhowmik, N.G. and Mazumder, B.S. (1990) Physical forces generated by barge-tow traffic within a navigable waterway. In: Chang, H.H. and Hill, J.C. (eds.), *Hydraulic Engineering*. American Society of Civil Engineers, New York, pp. 604–609.
- Bhowmik, N.G., Mazumder, B.S. and Soong, T.W. (1992) Return flows in large rivers associated with navigation traffic. In: Jennings, M. and Bhowmik, N.G. (eds.), *Hydraulic Engineering: Saving a Threatened Resource — In Search of Solutions*. American Society of Civil Engineers, New York, pp. 760–765.
- Bhowmik, N.G., Xia, R.J., Mazumder, B.S. and Soong, T.W. (1995) Return flow in rivers due to navigation traffic. *J. Hydraul. Eng.* **121**, 914–918.
- Bischoff, A. (2002) *Juvenile Fish Recruitment in the Large Lowland River Oder: Assessing the Role of Physical Factors and Habitat Availability*. Shaker Verlag, Aachen. 156 pp.
- Bischoff, A. and Wolter, C. (2001) Groyne heads as potential summer habitats for juvenile rheophilic fishes in the lower Oder, Germany. *Limnologica* **31**, 17–26.
- Blake, R.W. (1983) *Fish Locomotion*. Cambridge University Press, Cambridge. 208 pp.
- Blaxter, J.H.S. (1969) Swimming speeds of fish. *FAO Fish. Rep.* **62**, 69–100.
- Blaxter, J.H.S. (1986) Development of sense organs and behaviour of teleost larvae with special reference to feeding and predator avoidance. *Trans. Am. Fish. Soc.* **115**, 98–114.
- Blaxter, J.H.S. and Dickson, W. (1959) How fast can fish swim? *Scott. Fish. Bull.* **12**, 14–18.
- Bohle, H.W. (1995) *Spezielle Ökologie: Limnische Systeme*. Springer, Heidelberg. 267 pp.
- Boily, P. and Magnan, P. (2002) Relationship between individual variation in morphological characters and swimming costs in brook charr (*Salvelinus fontinalis*) and yellow perch (*Perca flavescens*). *J. Exp. Biol.* **205**, 1031–1036.
- Boon, P.J., Calow, P. and Petts, G.E. (eds.) (1992) *River Conservation and Management*. John Wiley & Sons, Chichester. 470 pp.
- Booth, R.K., McKinley, R.S., Økland, F. and Sisak, M.M. (1997) In-situ measurement of swimming performance of wild Atlantic salmon (*Salmo salar*) using radio-transmitted electromyogram signals. *Aquat. Living Resour.* **10**, 213–219.
- Bradford, M.J. (1997) An experimental study of stranding of juvenile salmonids on gravel bars and in side channels during rapid flow decreases. *Regul. Rivers: Res. Mgmt.* **13**, 395–401.
- Bradford, M.J., Taylor, G.C., Allan, J.A. and Higgins, P.S. (1995) An experimental study of stranding of juvenile coho salmon and rainbow trout during rapid flow decreases in winter condition. *North Am. J. Fish. Mgmt.* **15**, 473–479.
- Brett, J.R. (1964) The respiratory metabolism and swimming performance of young sockeye salmon. *J. Fish. Res. Board Can.* **21**, 1183–1226.
- Brett, J.R. and Glass, N.R. (1973) Metabolic rates and critical swimming speeds of sockeye salmon (*Oncorhynchus nerka*) in relation to size and temperature. *J. Fish. Res. Board Can.* **30**, 379–387.
- Brinke, W.B.M., Kruyt, N.M., Kroon, A. and van den Berg, J.H. (1999) Erosion of sediments between groynes in the River Waal as a result of navigation traffic. *Spec. Publ. Int. Ass. Sedimentologists* **28**, 147–160.
- Brookes, A. and Hanbury, R.G. (1990) Environmental impacts on navigable river and canal systems: a review of the British experience. *Bull. PIANC, S.I* **4**, 91–103.
- Brunke, M., Sukhodolov, A., Fischer, H., Wilezek, S., Engelhardt, C. and Pusch, M. (2002) Benthic and hyporheic habitats of a large lowland river (Elbe, Germany): influence of river engineering. *Verh. Internat. Verein. Limnol.* **28**, 153–156.

- Butler, P.J. and Day, N. (1993) The relationship between intracellular pH and swimming performance of brown trout exposed to neutral and sublethal pH. *J. Exp. Biol.* **176**, 271–284.
- Butler, P.J., Day, N. and Namba, K. (1992) Interactive effects of seasonal temperature and low pH on resting oxygen uptake and swimming performance of adult brown trout *Salmo trutta*. *J. Exp. Biol.* **165**, 195–212.
- Cada, G.F. (1990) A review of studies relating to the effect of propeller-type turbine passage on fish early life stages. *North Am. J. Fish. Mgmt.* **10**, 418–426.
- Colville, R.N., Hutchinson, E.J., Mindell, J.S. and Warren, R.F. (2001) The transport sector as a source of air pollution. *Atmospheric Environment* **35**, 1537–1565.
- Copp, G.H. (1989) The habitat diversity and fish reproductive function of floodplain ecosystems. *Env. Biol. Fish.* **26**, 1–27.
- Coutant, C.C. and Whitney, R.R. (2000) Fish behavior in relation to passage through hydropower turbines: a review. *Trans. Am. Fish. Soc.* **129**, 351–380.
- Cowx, I.G. and Welcomme, R. (eds.) (1998) *Rehabilitation of Rivers for Fish*. Fishing News Books, FAO, Rome. 260 pp.
- Daemrich, K.F., Mathias, H.J. and Zimmermann, C. (1996) Untersuchungen zur Bemessung von Deckwerken in Schiffahrtskanälen unter Wellenbelastung – Einfluß der Deckschichtdicke auf die Stabilität der Deckschicht. *Dresdner Wasserbauliche Mitteilungen* **9**, 1–10.
- D'Août, K. and Aerts, P. (1999) A kinematic comparison of forward and backward swimming in the eel *Anguilla anguilla*. *J. Exp. Biol.* **202**, 1511–1521.
- Domenici, P. (2001) The scaling of locomotor performance in predator-prey encounters: from fish to killer whales. *Comp. Biochem. Physiol. A* **131**, 169–182.
- Domenici, P. and Blake, R.W. (1997) The kinematics and performance of fish fast-start swimming. *J. Exp. Biol.* **200**, 1165–1178.
- Drucker, E.G. (1996) The use of gait transition speed in comparative studies of fish locomotion. *Amer. Zool.* **36**, 555–566.
- Drucker, E.G. and Lauder, G.V. (2000) A hydrodynamic analysis of fish swimming speed: wake structure and locomotor force in slow and fast labriform swimmers. *J. Exp. Biol.* **203**, 2379–2393.
- Duncan, A., Kubecka, J., Kett, S., Hanna, N. and Skeldon, J. (2001) Habitats of 0+ fry in an English lowland river. *Arch. Hydrobiol. Suppl.* **12**, 153–171.
- Ellerby, D.J., Spierts, I.L.Y. and Altringham, J.D. (2001) Slow muscle power output of yellow and silver phase European eels (*Anguilla anguilla* L.): changes in muscle performance prior to migration. *J. Exp. Biol.* **204**, 1369–1379.
- European Commission (2001) *WHITE PAPER – European Transport Policy for 2010: Time to Decide*. Office for Official Publications of the European Communities, Luxembourg. 119 pp.
- Farlinger, S. and Beamish, F.W.H. (1977) Effects of time and velocity increments on the critical swimming speed of largemouth bass (*Micropterus salmoides*). *Trans. Am. Fish. Soc.* **106**, 436–439.
- Farlinger, S. and Beamish, F.W.H. (1978) Changes in blood chemistry and critical swimming speed of largemouth bass, *Micropterus salmoides*, with physical conditioning. *Trans. Am. Fish. Soc.* **107**, 523–527.
- Flore, L., Keekeis, H. and Schiemer, F. (2001) Feeding, energetic benefit and swimming capabilities of 0+ nase (*Chondrostoma nasus* L.) in flowing water: an integrative laboratory approach. *Arch. Hydrobiol. Suppl.* **135**, 409–424.
- Frith, H.R. and Blake, R.W. (1995) The mechanical power output and hydromechanical efficiency of northern pike (*Esox lucius*) fast-starts. *J. Exp. Biol.* **198**, 1863–1873.
- Fry, F.E.J. and Cox, E.T. (1970) A relation of size to swimming speed in rainbow trout. *J. Fish. Res. Board Can.* **27**, 976–978.
- Fuehrer, M. (1998) Evaluation of the hydraulic load on waterways induced by navigation. *Mitteilungsblatt der Bundesanstalt für Wasserbau* **77**, 17–42.
- Fuehrer, M. and Pagel, W. (2000) Formparameter und Tiefgangseinflüsse auf die erreichbare Schiffsgeschwindigkeit und die Sohlströmung im allseitig begrenzten Fahrwasser (Ergebnisse der 3D-Modellierung der Schiffsumströmung nach FANKAN. *Mitteilungsblatt der Bundesanstalt für Wasserbau* **82**, 39–50.
- Fuiman, L.A. (1986) Burst swimming performance of larval zebra danios and the effects of diel temperature fluctuations. *Trans. Am. Fish. Soc.* **115**, 143–148.
- Fuiman, L.A. and Batty, R.S. (1997) What a drag it is getting cold: partitioning the physical and physiological effects of temperature on fish swimming. *J. Exp. Biol.* **200**, 1745–1755.
- Fuiman, L.A. and Magurran, A.E. (1994) Development of predator defences in fishes. *Rev. Fish Biol. Fish.* **4**, 145–183.
- Gamperl, A.K., Schnurr, D.L. and Stevens, E.D. (1991) Effect of a sprint-training protocol on acceleration performance in rainbow trout (*Salmo gairdneri*). *Can. J. Zool.* **69**, 578–582.
- Garner, P. (1999) Swimming ability and differential use of velocity patches by 0+ cyprinids. *Ecol. Freshw. Fish* **8**, 55–58.
- Garrad, P.N. and Hey, R.D. (1987) Boat traffic, sediment resuspension and turbidity in a broadland river. *J. Hydrol.* **95**, 289–297.
- Gaudin, P. (2001) Habitat shifts in juvenile riverine fishes. *Arch. Hydrobiol. Suppl.* **135**, 393–408.
- Glova, G.J. and McInerney, J.E. (1977) Critical swimming speeds of coho salmon (*Oncorhynchus kisutch*) fry to smolt stages in relation to salinity and temperature. *J. Fish. Res. Board Can.* **34**, 151–154.
- Goolish, E.M. (1991) Anaerobic swimming metabolism of fish: sit-and-wait versus active forager. *Physiol. Zool.* **64**, 485–501.
- Gore, J.A. and Petts, G.E. (eds.) (1989) *Alternatives in Regulated River Management*. CRC Press, Boca Raton, Florida. 344 pp.
- Graßl, H., Kokott, J., Kulessa, M., Luther, J., Nuscheler, F., Sauerborn, R., Schellnhuber, H.-J., Schubert, R. and Schulze, E.-D. (2002) *Charging the Use of Global Commons*. German Advisory Council on Global Change, Berlin, Special Report. 48 pp.
- Gregory, T.R. and Wood, C.M. (1998) Individual variations and interrelationships between swimming performance, growth rate, and feeding in juvenile rainbow trout (*Oncorhynchus mykiss*). *Can. J. Fish. Aquat. Sci.* **55**, 1583–1590.
- Gregory, T.R. and Wood, C.M. (1999) Interactions between individual feeding behaviour, growth, and swimming performance in juvenile rainbow trout (*Oncorhynchus mykiss*) fed different rations. *Can. J. Fish. Aquat. Sci.* **56**, 479–486.
- Grift, R. (2001) *How Fish Benefit from Floodplain Restoration Along the Lower River Rhine*. Ponsen & Looijen bv, Wageningen. 205 pp.
- Gutreuter, S., Dettmers, J.M. and Wahl, D.H. (1999) Abundance of Fishes in the Navigation Channels of the Mississippi and Illinois Rivers and Entrainment Mortality of Adult Fish Caused by Towboats. U.S. Geological Survey and Illinois Natural History Survey, ENV Report 29. 156 pp.
- Gutreuter, S., Dettmers, J.M. and Wahl, D.H. (2003) Estimating mortality rates of adult fishes from entrainment through the propellers of river towboats. *Trans. Am. Fish. Soc.* **132**, 647–661.
- Hadderingh, R.H. and Bakker, H.D. (1998) Fish mortality due to passage through hydroelectric power stations on the Meuse and Vecht Rivers. In: Jungwirth, M., Schmutz, S. and Weiss, S. (eds.), *Fish Migration and Fish Bypasses*. Fishing News Books, Blackwell Science, Oxford, pp. 315–328.

- Haefner, J.W. and Bowen, M.D. (2002) Physical-based model of fish movement in fish extraction facilities. *Ecol. Modelling* **152**, 227–245.
- Hale, M.E. (1999) Locomotor mechanics during early life history: effects of size and ontogeny on fast start performance of salmonid fishes. *J. Exp. Biol.* **202**, 1465–1479.
- Hammer, C. (1995) Fatigue and exercise tests with fish. *Comp. Biochem. Physiol. A* **112**, 1–20.
- Harper, D.G. and Blake, R.W. (1990) Fast start performance of rainbow trout *Salmo gairdneri* and northern pike *Esox lucius*. *J. Exp. Biol.* **150**, 321–342.
- Harper, D.G. and Blake, R.W. (1991) Prey capture and the fast start performance of northern pike *Esox lucius*. *J. Exp. Biol.* **155**, 175–192.
- Hawkins, D.K. and Quinn, T.P. (1996) Critical swimming velocity and associated morphology of juvenile coastal cutthroat trout (*Oncorhynchus clarki-clarki*), steelhead trout (*Oncorhynchus mykiss*), and their hybrids. *Can. J. Fish. Aquat. Sci.* **53**, 1487–1496.
- Heap, S.P. and Goldspink, G. (1986) Alterations to the swimming performance of carp, *Cyprinus carpio*, as a result of temperature acclimation. *J. Fish Biol.* **29**, 747–753.
- Hegggenes, J. and Traaen, T. (1988) Downstream migration and critical water velocities in stream channels for fry of four salmonid species. *J. Fish Biol.* **32**, 717–727.
- Heibaum, M. and Soyeaux, R. (2002) Traditional design patterns for calculation of forces on bottom and embankments and their use for fast ships for inland navigation. *Mitteilungen aus dem Franzius-Institut für Wasserbau und Küsteningenieurwesen* **88**, 100–119.
- Hertel, H. (1966) *Structure, Form, Movement*. New York: Reinhold Publishing Corp. 251 pp.
- Hochstein, A.B. and Adams Jr., E. (1989) Influence of vessel movements on stability of restricted channels. *J. Waterway, Port, Coastal, Ocean Eng.* **115**, 444–456.
- Hofbauer, J. (1965) Die Zusammensetzung der Brut- und Jungfischschwärme in dem zu einer Schifffahrtsstraße ausgebauten Main. *Z. Fischerei NF* **13**, 217–234.
- Holland, L.E. (1986) Effects of barge traffic on distribution and survival of ichthyoplankton and small fishes in the Upper Mississippi River. *Trans. Am. Fish. Soc.* **115**, 162–165.
- Holland, L.E. (1987) Effect of brief navigation-related dewaterings on fish eggs and larvae. *North Am. J. Fish. Mgmt.* **7**, 145–147.
- Holland, L.E. and Sylvester, J.R. (1983) Distribution of larval fishes related to potential navigation impacts on the Upper Mississippi River, Pool 7. *Trans. Am. Fish. Soc.* **112**, 293–301.
- Holmlund, C.M. and Hammer, M. (1999) Ecosystem services generated by fish populations. *Ecol. Econ.* **29**, 253–268.
- Houde, E.D. (1969) Sustained swimming ability of larvae of walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*). *J. Fish. Res. Board Can.* **26**, 1647–1659.
- Howard, T.E. (1975) Swimming performance of juvenile coho salmon (*Oncorhynchus kisutch*) exposed to bleached kraft pulp-mill effluent. *J. Fish. Res. Board Can.* **32**, 789–793.
- Howland, H.C. (1974) Optimal strategies for predator avoidance: the relative importance of speed and manoeuvrability. *J. Theor. Biol.* **47**, 333–350.
- Hüsig, A. and Linke, T. (1999) Grenzen der Einsatzmöglichkeiten schneller Binnenschiffe. *Binnenschifffahrt-ZfB* **4**, 1–9.
- Hüsig, A., Linke, T. and Zimmermann, C. (2000) Effects from supercritical ship operation on inland canals. *J. Waterway, Port, Coastal, Ocean Eng.* **126**, 130–135.
- Jackiewicz Jr., T.P. and Kuzminski, L.N. (1973) The effects of the interaction of outboard motors with the aquatic environment—a review. *Env. Res.* **6**, 436–454.
- Jähne, B., Köhler, H.-J., Rath, R. and Wierzimok, D. (1993) Measurement of the water wave amplitude by Digital Image Processing. *Mitteilungsblatt der Bundesanstalt für Wasserbau* **70**, 27–62.
- Jiang, T., Henn, R. and Sharma, S.D. (2002) Wash waves generated by ships moving on fairways of varying topography. *Proc. 24th Symposium on Naval Hydrodynamics*, Fukuoka, Japan, pp. 1–15.
- Jones, D.R., Kiceniuk, J.W. and Bamford, O.S. (1974) Evaluation of the swimming performance of several fish species from the Mackenzie River. *J. Fish. Res. Board Can.* **31**, 1641–1647.
- Jude, D.J., Tesar, F.J. and Tin, H.T. (1998) Spring distribution and abundance of larval fishes in the St. Marys River, with a note on potential effects of freighter traffic on survival of eggs and larvae. *J. Great Lakes Res.* **24**, 569–581.
- Justen, F. (2002) Inland waterway freight transport in 1995–2000 in the European Union. *Statistics in Focus Theme 7* **8**, 1–6.
- Karr, J.R. and Chu, E.W. (1999) *Restoring Life in Running Waters*. Island Press, Washington, D.C. 206 pp.
- Kaufmann, R. (1990) Respiratory cost of swimming in larval and juvenile cyprinids. *J. Exp. Biol.* **150**, 343–366.
- Kaufmann, R. and Wieser, W. (1992) Influence of temperature and ambient oxygen on the swimming energetics of cyprinid larvae and juveniles. *Env. Biol. Fishes* **33**, 87–95.
- Keen, J.E. and Farrell, A.P. (1994) Maximum prolonged swimming speed and maximum cardiac performance of rainbow trout, *Oncorhynchus mykiss*, acclimated to two different water temperatures. *Comp. Biochem. Physiol. A* **108**, 287–295.
- Kieffer, J.D. (2000) Limits to exhaustive exercise in fish. *Comp. Biochem. Physiol. A* **126**, 161–179.
- Kieffer, J.D. and Tufts, B.L. (1998) Effects of food deprivation on white muscle energy reserves in rainbow trout (*Oncorhynchus mykiss*): the relationships with body size and temperature. *Fish Physiol. Biochem.* **19**, 239–245.
- Killgore, K.J., Miller, A.C. and Conley, K.C. (1987) Effects of turbulence on yolk-sac larvae of paddlefish. *Trans. Am. Fish. Soc.* **116**, 670–673.
- Killgore, K.J., Maynard, S.T., Chan, M.D. and Morgan II, R.P. (2001) Evaluation of propeller-induced mortality on early life stages of selected fish species. *North Am. J. Fish. Mgmt.* **21**, 947–955.
- Koblickaya, A.F. (1981) *A Key for Identifying Young Freshwater Fishes*, 2nd ed. Light and Food Industry Publishing House, Moscow (in Russian). 208 pp.
- Kolok, A.S. (1991) Photoperiod alters the critical swimming speed of juvenile largemouth bass, *Micropterus salmoides*, acclimated to cold water. *Copeia* **1991**, 4, 1085–1090.
- Kolok, A.S. (1999) Interindividual variation in the prolonged locomotor performance of ectothermic vertebrates: a comparison of fish and herpetofaunal methodologies and a brief review of the recent fish literature. *Can. J. Fish. Aquat. Sci.* **56**, 700–710.
- Komarow, V.T. (1971) Speeds of fish movement. *Vestnik Zoologii* **4**, 67–71 (in Russian).
- Kubec, J. and Podzimek, J. (1996) *Wasserwege*. Verlag Werner Dausien, Hanau. 491 pp.
- Kuo, C.Y., Jordan, D.M., Ying, K.J., Loganathan, G.V. and Furry, J.C. (1989) Vessel induced physical effects in a navigation channel. In: Ports, M. (ed.), *Hydraulic Engineering*. American Society of Civil Engineers, New York, pp. 975–980.
- Law, T.C. and Blake, R.W. (1996) Comparison of the fast start performances of closely related, morphologically distinct

- threespine sticklebacks (*Gasterosteus* spp.). *J. Exp. Biol.* **199**, 2595–2604.
- Lelek, A. and Buhse, G. (1992) *Fische des Rheins – früher und heute*. Springer-Verlag, Heidelberg. 214 pp.
- Liddle, M.J. and Scorgie, H.R.A. (1980) The effects of recreation on freshwater plants and animals: a review. *Biol. Conserv.* **17**, 183–206.
- Lightfoot, G.W. and Jones, N.V. (1996) The relationship between the size of 0+ roach, *Rutilus rutilus*, their swimming capabilities, and distribution in an English river. *Folia Zool.* **45**, 355–360.
- Lindsey, C.C. (1978) Form, function and locomotory habits in fish. In: Hoar, W.S. and Randall, D.J. (eds.), *Fish Physiology*. Vol. VII *Locomotion*. Academic Press, New York, pp. 1–100.
- Linfield, R.S.J. (1985) The effect of habitat modification on freshwater fisheries in lowland areas of eastern England. In: Alabaster, J.S. (ed.), *Habitat Modification and Freshwater Fisheries*. Butterworths, London, pp. 147–156.
- Linke, T., Scheffermann, J. and Zimmermann, C. (2002) Limitations for ship speed due to forces on bottom and embankments. *Mitteilungen aus dem Franziskus-Institut für Wasserbau und Küsteningenieurwesen* **88**, 80–87.
- Mann, R.H.K. and Bass, J.A.B. (1997) The critical water velocities of larval roach (*Rutilus rutilus*) and dace (*Leuciscus leuciscus*) and implications for river management. *Regul. Rivers: Res. Mgmt.* **13**, 295–301.
- Maynard, S.T. (1999) *Comparison of NAVEFF Model to Field Return Velocity and Drawdown Data*. U.S. Army Corps of Engineers, Upper Mississippi River–Illinois Waterway System Navigation Study. ENV Report 14. 46 pp.
- Maynard, S.T. (2000) Power versus speed for shallow draft navigation. *J. Waterway, Port, Coastal, Ocean Eng.* **126**, 103–106.
- Maynard, S.T. and Martin, S.K. (1997) *Physical Forces Study, Kampsville, Illinois Waterway*. U.S. Army Corps of Engineers, Upper Mississippi River–Illinois Waterway System Navigation Study, ENV Report 3. 171 pp.
- Maynard, S.T. and Siemsen, T.S. (1991) Return velocities induced by shallow draft navigation. In: Shane, R.M. (ed.), *Hydraulic Engineering*. American Society of Civil Engineers, New York, pp. 894–899.
- Mazumder, B.S., Bhowmik, N.G. and Soong, T.W. (1993) Turbulence in rivers due to navigation traffic. *J. Hydraul. Eng.* **119**, 581–597.
- McCleave, J.D. (1980) Swimming performance of European eel (*Anguilla anguilla* (L.)) elvers. *J. Fish Biol.* **16**, 445–452.
- McDonald, D.G., McFarlane, W.J. and Milligan, C.L. (1998) Anaerobic capacity and swim performance of juvenile salmonids. *Can. J. Fish. Aquat. Sci.* **55**, 1198–1207.
- McLaughlin, R.L. and Noakes, D.L.G. (1998) Going against the flow: an examination of the propulsive movements made by young brook trout in streams. *Can. J. Fish. Aquat. Sci.* **55**, 853–860.
- Morgan II, R.P., Ulanowicz, R.E., Rasin Jr., V.J., Noc, L.A. and Gray, G.B. (1976) Effects of shear on eggs and larvae of striped bass, *Morone saxatilis*, and white perch, *M. americana*. *Trans. Am. Fish. Soc.* **105**, 149–154.
- Moyle, P.B. and Cech Jr., J.J. (1988) *Fishes: An Introduction to Ichthyology*. 2nd edn. Prentice Hall, Englewood Cliffs. 559 pp.
- Mueller, G. (1980) Effects of recreational river traffic on nest defence by longear sunfish. *Trans. Am. Fish. Soc.* **109**, 248–251.
- Müller, U.K. and Videler, J.J. (1996) Inertia as a 'safe harbour': do fish larvae increase length growth to escape viscous drag? *Rev. Fish Biol. Fish.* **6**, 353–360.
- Müller, U.K., Stamhuis, E.J. and Videler, J.J. (2000) Hydrodynamics of unsteady fish swimming and the effects of body size: comparing the flow fields of fish larvae and adults. *J. Exp. Biol.* **203**, 193–206.
- Müller, U.K., Smit, J., Stamhuis, E.J. and Videler, J.J. (2001) How the body contributes to the wake in undulatory fish swimming: Flow fields of a swimming eel (*Anguilla anguilla*). *J. Exp. Biol.* **204**, 2751–2762.
- Murphy, K., Willby, N.J. and Eaton, J.W. (1995) Ecological impacts and management of boat traffic on navigable inland waterways. In: Harper, D.M. and Ferguson, A.J.D. (eds.), *The Ecological Basis for River Management*. John Wiley & Sons, Chichester, pp. 427–442.
- Nielsen, L.A., Sheehan, R.J. and Orth, D.J. (1986) Impacts of navigation on riverine fish production in the United States. *Pol. Arch. Hydrobiol.* **33**, 277–294.
- Odom, M.C., Orth, D.J. and Nielsen, L.A. (1992) Investigation of barge-associated mortality of larval fishes in the Kanawha River. *Virginia J. Sci.* **43**, 41–45.
- Oebius, H. (2000a) Navigation as cause for man-made changes of the river morphology and ecology of water bodies, and measures to limit these effects. *Angewandte Landschaftsökologie* **37**, 233–238.
- Oebius, H. (2000b) Charakterisierung der Einflussgrößen Schiffsumströmung und Propellerstrahl auf die Wasserstraßen. *Mitteilungsblatt der Bundesanstalt für Wasserbau* **82**, 7–22.
- Ohlmer, W. and Schwartzkopff, J. (1959) Schwimmgeschwindigkeiten von Fischen aus stehenden Binnengewässern. *Naturwissenschaften* **46**, 362–363.
- Ojanguren, A.F. and Braña, F. (2000) Thermal dependence of swimming endurance in juvenile brown trout. *J. Fish Biol.* **56**, 1342–1347.
- Osse, J.W.M. and Drost, M.R. (1989) Hydrodynamics and mechanics of fish larvae. *Pol. Arch. Hydrobiol.* **36**, 455–465.
- Otto, R.G. and O'Hara Rice, J. (1974) Swimming speeds of yellow perch (*Perca flavescens*) following an abrupt change in environmental temperature. *J. Fish. Res. Board Can.* **31**, 1731–1734.
- Pavlov, D.S. (1989) *Structures Assisting the Migrations of Non-Salmonid Fish: USSR*. FAO Fish. Tech. Pap., No. 308. Rome. FAO. 97 pp.
- Pavlov, D.S., Sbikin, Y.N., Vashchinnikov, A.E. and Mochek, A.D. (1972) The effect of light intensity and water temperature on current velocities critical to fish. *Voprosy Ikhtologii* **12**, 769–778 (in Russian).
- Pearsons, T.N., Li, H.W. and Lamberti, G.A. (1992) Influence of habitat complexity on resistance to flooding and resilience of stream fish assemblages. *Trans. Am. Fish. Soc.* **121**, 427–436.
- Petersen, R.H. (1974) Influence of Fenitrothion on swimming velocities of brook trout (*Salvelinus fontinalis*). *J. Fish. Res. Board Can.* **31**, 1757–1762.
- Petts, G.E. (1985) *Impounded Rivers: Perspectives for Ecological Management*. John Wiley & Sons, New York. 296 pp.
- Petts, G.E., Moller, H. and Roux, A.L. (eds.) (1989) *Historical Change of Large Alluvial Rivers: Western Europe*. John Wiley & Sons, Chichester. 335 pp.
- Pinder, A.C. (2001) *Keys to Larval and Juvenile Stages of Coarse Fishes from Fresh Waters in the British Isles*. Freshwater Biological Association, Scientific Publication No 60. 136 pp.
- Plaut, I. (2000) Effects of fin size on swimming performance, swimming behaviour and routine activity of zebrafish *Danio rerio*. *J. Exp. Biol.* **203**, 813–820.
- Plaut, I. (2001) Critical swimming speed: its ecological relevance. *Comp. Biochem. Physiol. A* **131**, 41–50.
- Pygott, J.R., O'Hara, K. and Eaton, J.W. (1990) Fish community structure and management in navigated British canals. In: van Densen, W.L.T., Steinmetz, B. and Hughes, R.H. (eds.),

- Management of Freshwater Fisheries*. Pudoc, Wageningen, pp. 547–557.
- Randall, D. and Brauner, C. (1991) Effects of environmental factors on exercise in fish. *J. Exp. Biol.* **160**, 113–126.
- Reidy, S.P., Kerr, S.R. and Nelson, J.A. (2000) Aerobic and anaerobic swimming performance of individual Atlantic cod. *J. Exp. Biol.* **203**, 347–357.
- Rodriguez, J.F., Admiraal, D.M., Lopez, F. and Garcia, M.H. (2002) Unsteady bed shear stresses induced by navigation: laboratory observations. *J. Hydraul. Eng.* **128**, 515–526.
- Rome, L.C., Funke, R.P., Alexander, R.M., Lutz, G., Aldridge, H., Scott, F. and Freedman, M. (1988) Why animals have different muscle fiber types? *Nature* **335**, 824–827.
- Rosen, R.A. and Hales, D.C. (1980) Occurrence of scarred paddlefish in the Missouri River, South Dakota-Nebraska. *The Progressive Fish Culturist* **42**, 82–85.
- Saltveit, S.J., Halleraker, J.H., Arnekleiv, J.V. and Harby, A. (2001) Field experiments on stranding in juvenile Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) during rapid flow decreases caused by hydropneaking. *Regul. Rivers: Res. Mgmt.* **17**, 609–622.
- Sand-Jensen, K. and Pedersen, O. (1999) Velocity gradients and turbulence around macrophyte stands in streams. *Freshw. Biol.* **42**, 315–328.
- Scheidegger, K.J. and Bain, M.B. (1995) Larval fish distribution and microhabitat use in free-flowing and regulated rivers. *Copeia* **1995**, 1, 125–135.
- Schiemer, F., Jungwirth, M. and Imhof, G. (1994) *Die Fische der Donau – Gefährdung und Schutz*. Bundesministerium für Umwelt, Jugend und Familie, Wien. 160 pp.
- Schiemer, F., Keckeis, H., Winkler, G. and Flore, L. (2001) Large rivers: the relevance of ecotonal structure and hydrological properties for the fish fauna. *Arch. Hydrobiol. Suppl.* **135**, 487–508.
- Schlosser, I.J. (1985) Flow regime, juvenile abundance, and the assemblage structure of stream fishes. *Ecology* **66**, 1484–1490.
- Sfakiotakis, M., Lane, D.M. and Davies, J.B.C. (1999) Review of fish swimming modes for aquatic locomotion. *IEEE J. Oceanic Eng.* **24**, 237–252.
- Simon, T.P. (ed.) (1999) *Assessing the Sustainability and Biological Integrity of Water Resources Using Fish Communities*. CRC Press, Boca Raton. 610 pp.
- Soong, T.W. and Bhowmik, N.G. (1992) Characteristics of waves and drawdown generated by barge traffic on the Upper Mississippi River System. In: Jennings, M. and Bhowmik, N.G. (eds.), *Hydraulic Engineering: Saving a Threatened Resource – In Search of Solutions*. American Society of Civil Engineers, New York, pp. 672–676.
- Sorensen, R.M. (1997) *Predicting of Vessel-Generated Waves with Reference to Vessels Common to the Upper Mississippi River System*. U.S. Army Corps of Engineers, Upper Mississippi River – Illinois Waterway System Navigation Study, ENV Report 4. 50 pp.
- Sparks Companies (2002) *Upper Mississippi River and Illinois Waterway Navigation Study. Economic Scenarios and Resulting Demand for Barge Transportation*. Sparks Companies Inc., Memphis, Tennessee, Final Report. 77 pp.
- Sprengel, G. and Lichtenberg, H. (1991) Infection by endoparasites reduces maximum swimming speed of European smelt *Osmerus eperlanus* and European eel *Anguilla anguilla*. *Dis. Aquat. Org.* **11**, 31–35.
- Staas, S. (1997) Das Jungfischauftreten im Niederrhein und in angrenzenden Nebengewässern. *LÖBF-Schriftenreihe* **12**, 5–114.
- Stahlberg, S. (1986) Das Schwimmverhalten von Bachschmerle (*Noemacheilus barbatulus*) und Gründling (*Gobio gobio*) im Strömungskanal. *Mitteilungen des Instituts für Wasserwirtschaft, Hydrologie und landwirtschaftlichen Wasserbau der Universität Hannover* **61**, 219–296.
- Stahlberg, S. and Peckmann, P. (1987) The critical swimming speed of small teleost fish species in a flume. *Arch. Hydrobiol.* **110**, 179–193.
- Stockstill, R.L. and Berger, R.C. (2001) Simulating barge drawdown and currents in channel and backwater areas. *J. Waterway, Port, Coastal, Ocean Eng.* **127**, 290–298.
- Taylor, E.B. and Foote, C.J. (1991) Critical swimming velocities of juvenile sockeye salmon and kokanee, the anadromous and non-anadromous forms of *Oncorhynchus nerka* (Walbaum). *J. Fish Biol.* **38**, 407–419.
- Taylor, E.B. and MacPhail, J.D. (1985) Variation in burst and prolonged swimming performance among British Columbia populations of coho salmon, *Oncorhynchus kisutch*. *Can. J. Fish. Aquat. Sci.* **42**, 2029–2033.
- Taylor, E.B. and MacPhail, J.D. (1986) Prolonged and burst swimming in anadromous and freshwater threespined stickleback, *Gasterosteus aculeatus*. *Can. J. Zool.* **64**, 416–420.
- Taylor, S.E., Egginton, S. and Taylor, E.W. (1996) Seasonal temperature acclimatisation of rainbow trout: cardiovascular and morphometric influences on maximal sustainable exercise level. *J. Exp. Biol.* **199**, 835–845.
- Thornton, C.I., Abt, S.R., Morris, C.E. and Fischenich, J.C. (2000) Calculating shear stress at channel-overbank interfaces in straight channels with vegetated floodplains. *J. Hydraul. Eng.* **126**, 929–936.
- Toeffer, C.S., Fisher, W.L. and Haubelt, J.A. (1999) Swimming performance of the threatened leopard darter in relation to road culverts. *Trans. Am. Fish. Soc.* **128**, 155–161.
- Tsukamoto, K., Kajihara, T. and Nishiwaki, M. (1975) Swimming ability of fish. *Bull. Jap. Soc. Scient. Fish.* **41**, 167–174.
- Turnpenny, A.W.H. (1998) Mechanisms of fish damage in low-head turbines: an experimental appraisal. In: Jungwirth, M., Schmutz, S. and Weiss, S. (eds.), *Fish Migration and Fish Bypasses*. Fishing News Books, Blackwell Science, Oxford, pp. 300–314.
- United Nations (1997) *Kyoto Protocol to the United Nations Framework Convention on Climate Change*. United Nations, New York, FCCC/CP/1997/L.7/Add.1. 20 pp.
- Van Damme, R. and van Dooren, T.J.M. (1999) Absolute versus per unit body length speed of prey as an estimator of vulnerability to predation. *Anim. Behav.* **57**, 347–352.
- Videler, J.J. (1993) *Fish Swimming*. Chapman & Hall, London. 260 pp.
- Videler, J.J. and Wardle, C.S. (1991) Fish swimming stride by stride: speed limits and endurance. *Rev. Fish Biol. Fish.* **1**, 23–40.
- Vitousek, P.M., Mooney, H.A., Lubchenco, J. and Melillo, J.M. (1997) Human domination of earth's ecosystems. *Science* **277**, 494–499.
- Vogel, S. (1994) *Life in Moving Fluids: The Physical Biology of Flow*, 2nd ed. Princeton University Press, Princeton. 484 pp.
- Wakeling, J.M., Kemp, K.M. and Johnston, I.A. (1999) The biomechanics of fast-starts during the ontogeny in the common carp *Cyprinus carpio*. *J. Exp. Biol.* **202**, 3057–3067.
- Walker, J.A. (2000) Does a rigid body limit manoeuvrability? *J. Exp. Biol.* **203**, 3391–3396.
- Wardle, C.S. (1975) Limit of fish swimming speed. *Nature* **255**, 725–727.
- Wardle, C.S. (1980) Effects of temperature on the maximum swimming speed of fishes. In: Ali, M.A. (ed.), *Environmental Physiology of Fishes*. NATO Advanced Study Institute Series,

- Series A: Life Sciences, Plenum Press, New York, pp. 519–531.
- Webb, P.W. (1975a) Hydrodynamics and energetics of fish propulsion. *Bull. Fish. Res. Board Can.* **190**, 1–159.
- Webb, P.W. (1975b) Acceleration performance of rainbow trout *Salmo gairdneri* and green sunfish *Lepomis cyanellus*. *J. Exp. Biol.* **63**, 451–465.
- Webb, P.W. (1976) The effect of size on the fast-start performance of rainbow trout *Salmo gairdneri* and a consideration of piscivorous predator-prey interactions. *J. Exp. Biol.* **65**, 157–177.
- Webb, P.W. (1978) Fast-start performance and body form in seven species of teleost fish. *J. Exp. Biol.* **74**, 211–226.
- Webb, P.W. (1982) Avoidance responses of fathead minnow to strikes by four teleost predators. *J. Comp. Physiol. A* **147**, 371–378.
- Webb, P.W. (1984a) Form and function in fish swimming. *Sci. Amer.* **251**, 58–68.
- Webb, P.W. (1984b) Body and fin form and strike tactics of four teleost predators attacking fathead minnow (*Pimephales promelas*) prey. *Can. J. Fish. Aquat. Sci.* **41**, 157–165.
- Webb, P.W. (1986a) Kinematics of lake sturgeon, *Acipenser fulvescens*, at cruising speeds. *Can. J. Zool.* **64**, 2137–2141.
- Webb, P.W. (1986b) Effect of body form and response threshold on the vulnerability of four species of teleost prey attacked by largemouth bass (*Micropterus salmoides*). *Can. J. Fish. Aquat. Sci.* **43**, 763–771.
- Webb, P.W. and Weihs, D. (1983) *Fish Biomechanics*. Praeger Pub., New York. 398 pp.
- Webb, P.W. and Weihs, D. (1986) Functional locomotor morphology of early life history stages of fishes. *Trans. Am. Fish. Soc.* **115**, 115–127.
- Whoriskey, F.G. and Wootton, R.J. (1987) The swimming endurance of threespine sticklebacks, *Gasterosteus aculeatus* L., from the Afon Rheidol, Wales. *J. Fish Biol.* **30**, 335–339.
- Wieser, W. and Kaufmann, R. (1998) A note on interactions between temperature, viscosity, body size and swimming energetics in fish larvae. *J. Exp. Biol.* **201**, 1369–1372.
- Willby, N.J. and Eaton, J. W. (1996) Backwater habitats and their role in nature conservation on navigable waterways. *Hydrobiologia* **340**, 333–338.
- Wolter, C. (2001a) Rapid changes of fish assemblages in artificial lowland waterways. *Limnologia* **31**, 27–35.
- Wolter, C. (2001b) Conservation of fish species diversity in navigable waterways. *Landscape and Urban Planning* **53**, 135–144.
- Wolter, C. and Vileinskas, A. (1997) Perch (*Perca fluviatilis*) as an indicator species for structural degradation in regulated rivers and canals in the lowlands of Germany. *Ecol. Freshw. Fish* **6**, 174–181.
- Wootton, R.L. (1990) *Ecology of Teleost Fishes*. Chapman & Hall, London. 404 pp.
- WSD Ost (2002) *Statistischer Verkehrsbericht 2001. Binnenschifffahrt in Zahlen*. Wasser- und Schifffahrtsdirektion (WSD) Ost, Berlin. 35 pp.
- Zauner, G. and Schiemer, F. (1992) Auswirkung der Schifffahrt auf die Fischfauna – aufgezeigt am Beispiel der österreichischen Donau. *Landschaftswasserbau* **14**, 133–152.
- Zauner, G. and Schiemer, F. (1994) Auswirkung der Schifffahrt auf die Fischfauna großer Fließgewässer. *Wiss. Mitt. Niederöstr. Landesmuseum* **8**, 271–285.
- Zerrath, H. (1996) Sprintleistungen einheimischer Klein- und Jungfische in Sohlgleitenmodellen – Daten zur Bewertung von Fischaufstiegshilfen. *Fischökologie* **9**, 27–48.

Appendix

Table 1. Critical and burst swimming speeds of freshwater fishes (BL = Body length, TL = Total length, T = Temperature)

Species	Length (mm)	Swimming performance			Time (s)	Temp (°C)	Reference
		U_{crit} cm s ⁻¹	BL s ⁻¹	U_{max} cm s ⁻¹	BL s ⁻¹		
<i>Abramis balticus</i>	17–59	22–51 ^c					Pavlov, 1989
<i>Abramis bjoerkna</i>	22			30	15		Radtke, 1964*
<i>Abramis brama</i>	120/280	87/96				18	Ohlmer and Schwartzkopf, 1959
<i>Acipenser fulvescens</i>	157	38.6				15	Webb, 1986a
<i>Acipenser gueldenstaedti</i>	40–69	22–29 ^c		2.45		18–22	Pavlov et al., 1972
<i>Acipenser stellatus</i>	55–70	21–26 ^c				18–22	Pavlov et al., 1972
<i>Alburnoides bipunctatus</i>	33–60			10.1		180	Cowx and Welcomme, 1998
<i>Alburnus alburnus</i>	19–34	31–53 ^c					Pavlov, 1989
<i>Anguilla anguilla</i>	600			114	1.9	2	Blaxter and Dickson, 1959
<i>Anguilla anguilla</i>	72	54		7.5		18	McCleave, 1980
<i>Anguilla anguilla</i>	170–450	–0.82 + 0.45 ln (TL)				120–180	Sprengel and Lichtenberg, 1991
<i>Anguilla anguilla</i>	220	31.8		1.58		18–22	D'Aodis and Aerts, 1999
<i>Anguilla rostrata</i>	56	30		40		17–23	Barbin and Krueger, 1994
<i>Barbatula barbatula</i>	91	53.0/60.8		14.2		4/20	Stahlberg, 1986
<i>Barbatula barbatula</i>	110	60.8		5.5		180	Stahlberg and Peckmann, 1987
<i>Barbatula barbatula</i>	22–42	22.5–38 ^c				18–22	Pavlov et al., 1972
<i>Barbus barbus</i>	19–30			11.5		180	Cowx and Welcomme, 1998
<i>Carassius auratus</i>	90			138	15.1	2	Blaxter and Dickson, 1959
<i>Carassius auratus</i>	67–213	42–48		74–200	11–9.4	1/20	Bainbridge, 1960
<i>Carassius auratus</i>	50–210			10		15	Blaxter, 1969
<i>Carassius auratus</i>	180			108	8		Hertel, 1966
<i>Carassius carassius</i>	100				11.4	6	Tsukamoto et al., 1975
<i>Carassius carassius</i>	18–42	20–49 ^c		226	9.8	<1	Pavlov, 1989
<i>Carassius gibelio</i>	230						Komarow, 1971
<i>Catostomus catostomus</i>	40–530 ^b	11.03*TL ^{0.53}				600	Jones et al., 1974
<i>Catostomus commersoni</i>	170–370 ^b	10.03*TL ^{0.55}				600	Jones et al., 1974
<i>Chalcaburnus chalcoides</i>	125			187	15	<1	Komarow, 1971
<i>Chalcaburnus chalcoides</i>	9/13/17	6.3/7.3/8.7				15	Wieser and Kaufmann, 1998
<i>Chalcaburnus chalcoides</i>	9/13/17	7.8/10/11.6				20	Wieser and Kaufmann, 1998
<i>Chondrostoma nasus</i>	15–45	4.39 + 0.456 TL (cm s ⁻¹)				16	Flore et al., 2001
<i>Cobitis taenia</i>	34–71	25–42 ^c					Pavlov, 1989
<i>Coregonus autumnalis</i>	421 ^b	80				600	Jones et al., 1974
<i>Coregonus elupeaformis</i>	60–510 ^b	18.2*TL ^{0.35}				600	Jones et al., 1974

Table 1. Continued

Species	Length (mm)	Swimming performance				Time (s)	Temp (°C)	Reference
		U_{crit} cm s ⁻¹	U_{crit} BL s ⁻¹	U_{max} cm s ⁻¹	U_{max} BL s ⁻¹			
<i>Coregonus nasus</i>	60–330 ^b	$9.7 \pm FL^{0.45}$				600	12–20	Jones et al., 1974
<i>Coregonus sardinella</i>	295 ^b	60				600	12–20	Jones et al., 1974
<i>Cottus cognatus</i>	82				9.4	0.081	±5	Webb, 1978
<i>Cottus gobio</i>	16–41	15–34 ^c						Pavlov, 1989
<i>Cyprinus carpio</i>	350			226	8.2	<1		Komarow, 1971
<i>Cyprinus carpio</i>	70–130		2.43/2.63		4.1 ^d		10/20	Heup and Goldspink, 1986
<i>Cyprinus carpio</i>	36–77	86–98	13.6–15.6	166.4	26.7	3–4.5/1	16–18	Zerrath, 1996
<i>Cyprinus carpio</i>	10–62.5			$3.71 \times FL^{0.584}$ (m s ⁻¹); FL in m		<0.5	20–21	Wakeling et al., 1999
<i>Danio rerio</i>	3.6			1.8–2.4	50–66	<1	21–30	Fuiman, 1986
<i>Danio rerio</i>	31.8–39.7 ^a	56 ± 4.8	15.5 ^a			300	28	Plaut, 2000
<i>Exocoetidae</i>	425	297					±8	Ohlmer and Schwartzkopff, 1959
<i>Exocoetidae</i>	170–200			150–210	7.5–12.5			Hertel, 1966
<i>Exocoetidae</i>	120–620 ^b	$4.9 \times FL^{0.55}$	600				12–20	Jones et al., 1974
<i>Exocoetidae</i>	217				7.2	0.115	±5	Webb, 1978
<i>Exocoetidae</i>	380			397	8.2–10.5	0.1–0.2		Harper and Blake, 1991
<i>Exocoetidae</i>	412 ^b			280/340		0.13/0.16	8–12	Firth and Blake, 1995
<i>Etheostoma caeruleum</i>	62				14.4	0.056	±5	Webb, 1978
<i>Gasterosteus aculeatus</i>	44.4 ^a	108		159		0.05	±5	Law and Blake, 1996
<i>Gasterosteus aculeatus</i>	60	66.1	11.1					Taylor and MacPhail, 1986
<i>Gasterosteus aculeatus</i>	55	36.3	6.6			180	18	Stahlberg and Peckmann, 1987
<i>Gasterosteus aculeatus</i>	50	35	7			60	20	Whoriskey and Wootton, 1987
<i>Gasterosteus aculeatus</i>	33–74	80–83	15.8–16.6	145	33.5	4.5–5/1	16–18	Zerrath, 1996
<i>Gobio gobio</i>	61–80	31–37/43–51					3/20	Pavlov et al., 1972
<i>Gobio gobio</i>	116	43.0/55.0	3.6/4.66		19.7	600	4/20	Stahlberg, 1986
<i>Gobio gobio</i>	118	45.6/55.0	3.9/4.7			180	4/18	Stahlberg and Peckmann, 1987
<i>Gobio gobio</i>	53–95	106–119	15–16.7	268	36.2	5/1	16–18	Zerrath, 1996
<i>Gobio gobio</i>	28–50		8.85			180	15–16	Cox and Welcomme, 1998
<i>Gymnocephalus cernuus</i>	105			133	12.7	<1		Komarow, 1971
<i>Hiodon alosoides</i>	225 ^b	60				600	12–20	Jones et al., 1974
<i>Huso huso</i>	52–70	21–29 ^c						Pavlov, 1989
<i>Hypophthalmichthys molitrix</i>	270			248	9.2	<1		Komarow, 1971
<i>Lepomis cyanellus</i>	80				8.4	0.079	±5	Webb, 1975b
<i>Lepomis cyanellus</i>	80			150	18.8	0.08		Beamish, 1978
<i>Lepomis macrochirus</i>	153				8.5	0.088	±5	Webb, 1978
<i>Lepomis macrochirus</i>	64				15.8	<1	±5	Webb, 1986b

Table 1. Continued

Species	Length (mm)	Swimming performance			Time (s)	Temp (°C)	Reference
		U_{crit} cm s ⁻¹	U_{crit} BL s ⁻¹	U_{max} cm s ⁻¹			
<i>Leucaspisus delineatus</i>	30-41	36-55 ^c			18-22		Pavlov et al., 1972
<i>Leucaspisus delineatus</i>	51	22.7/38.6	4.5/7.7		180	4/18	Stahlberg and Peckmann, 1987
<i>Leuciscus cerphatus</i>	48-64	82-92	15.2-17	214.5	4-6/1-16-18		Zerrath, 1996
<i>Leuciscus cerphatus</i>	66-87	96-106	12.5-13.7	376.2	4-6/1-16-18		Zerrath, 1996
<i>Leuciscus cerphatus</i>	6-43 ^a	0.45 ± 0.23 T + 0.55 SL (cm s ⁻¹)			180	8-22	Garnier, 1999
<i>Leuciscus leuciscus</i>	100-214	46-90	4.4-4.2	110-240	1/20	14	Bainbridge, 1960
<i>Leuciscus leuciscus</i>	8.3-17.3	-19.39 + 1.46 TL + 0.9 T (cm s ⁻¹)		11.2-11	180	13-20	Mann and Bass, 1997
<i>Leuciscus leuciscus</i>	9-25	10.3			180	15-16	Cox and Welcomme, 1998
<i>Leuciscus leuciscus</i>	6-43 ^a	-7.4 + 1.0 T + 0.83 SL (cm s ⁻¹)			180	8-22	Garnier, 1999
<i>Lota lota</i>	120-620 ^b	30.6*FL ^{0.07}			600	12-20	Jones et al., 1974
<i>Micropterus salmoides</i>	102 ^b	50 ^c	5 ^c		300	25	Farlinger and Beamish, 1977
<i>Micropterus salmoides</i>	142 ^b	47.7 ^c			1800	25	Farlinger and Beamish, 1978
<i>Micropterus salmoides</i>	51			18.8	<1	15	Webb, 1986b
<i>Micropterus salmoides</i>	93-128 ^b		2.22/2.9/3.6 ^c		1200	5/40/17	Kolok, 1991
<i>Notropis atherinoides</i>	65 ^a	59			600	12-20	Jones et al., 1974
<i>Notropis cornutus</i>	107			10.7	0.078-15		Webb, 1978
<i>Oncochymus clarki</i>	87-100 ^b	300-540	5-58		900	10	Hawkins and Quinn, 1996
<i>Oncochymus kisutch</i>	360-610		6-9				Weaver, 1963*
<i>Oncochymus kisutch</i>	64.3		5-63		1+h	13	Howard, 1975
<i>Oncochymus kisutch</i>	40-60 ^b		3.5/7.3	40	1+h	3/23	Glova and McIhenny, 1977
<i>Oncochymus kisutch</i>	80-120 ^b		3.5/5.5	65	1+h	3/23	Glova and McIhenny, 1977
<i>Oncochymus kisutch</i>	55 ^a	62.9-74.1		102.3-104.7	13.5		Taylor and McPhail, 1985
<i>Oncochymus kisutch</i>	19-32			14-100 ^c	<0.2	12	Hale, 1999
<i>Oncochymus kisutch</i>	32-72			35-160 ^c	<0.2	12	Hale, 1999
<i>Oncochymus mykiss</i>	103-280			105-270/32-73	1/20	14	Bainbridge, 1960
<i>Oncochymus mykiss</i>	610-820	430-830	7-13	10.2-7.6/3.1-2.6			Weaver, 1963*
<i>Oncochymus mykiss</i>	48/350 ^{b,d}				60	10	Fry and Cox, 1970
<i>Oncochymus mykiss</i>	305.8 ^b	66.57	9/5.5		600	12-20	Jones et al., 1974
<i>Oncochymus mykiss</i>	143			8.5	0.078-15		Webb, 1975b
<i>Oncochymus mykiss</i>	96/150/204			21/15/10.5	<1	15	Webb, 1976
<i>Oncochymus mykiss</i>	245-387			229-265	<1	15	Webb, 1976
<i>Oncochymus mykiss</i>	195			8.1	0.114-15		Webb, 1978
<i>Oncochymus mykiss</i>	318			8.7	0.125-15-20		Harper and Blake, 1990
<i>Oncochymus mykiss</i>	95			13.7	0.074-10		Gampert et al., 1991

Table 1. Continued

Species	Length (mm)	Swimming performance			Time (s)	Temp (°C)	Reference
		U_{crit} $cm\ s^{-1}$	U_{crit} BL s^{-1}	U_{max} $cm\ s^{-1}$	U_{max} BL s^{-1}		
<i>Oncorhynchus mykiss</i>	87–100 ^b		7.69			900	Hawkins and Quinn, 1996
<i>Oncorhynchus mykiss</i>	87 ^b		6			180/220	Gregory and Wood, 1998
<i>Oncorhynchus nerka</i>	162	58	3.65			1200	Brett, 1964
<i>Oncorhynchus nerka</i>	188	76.9	4.12			1200	Brett, 1964
<i>Oncorhynchus nerka</i>	195	74.1	3.9			1200	Brett, 1964
<i>Oncorhynchus nerka</i>	77–128	51.5–59.8	4.2–6.7			1 h	Brett and Glass, 1973
<i>Oncorhynchus nerka</i>	56–98	37.1–64.4	8.2–5.9			1 h	Brett and Glass, 1973
<i>Oncorhynchus nerka</i>	530–614	127–136	2.1–2.4			1 h	Brett and Glass, 1973
<i>Oncorhynchus nerka</i>	77.7 ^b	53.3/60.1 ^f	7.3/8.3 ^f			1200	Taylor and Foote, 1991
<i>Oncorhynchus tshawytscha</i>	510–970	550–680	7–11				Weaver, 1963*
<i>Oncorhynchus tshawytscha</i>	21–33/39–65			16–100/35–160 ^c		<0.2	Hale, 1999
<i>Osmorus eperlanus</i>	50–170	–0.16 + 0.24 ln (TL)				120–180	Sprengel and Lütkenberg, 1991
<i>Perca flavescens</i>	7.5/10.5/13.5	1.4/3.2/4.6	1.87/3.05/3.41			1 h	Houde, 1969
<i>Perca flavescens</i>	100 ^d	33.5				900	Otto and O'Hara-Rice, 1974
<i>Perca flavescens</i>	155			7.4		0–103	Webb, 1978
<i>Perca fluviatilis</i>	100/220	121/126				18	Ohlmer and Schwartzkopff, 1959
<i>Perca fluviatilis</i>	115			145		<1	Komarow, 1971
<i>Perca fluviatilis</i>	46–64	56–60 ^c				18–22	Pavlov et al., 1972
<i>Percopsis omiscomaycus</i>	72 ^b	55				12–20	Jones et al., 1974
<i>Petromyzon marinus</i>	123–148	20–60				1800	5–15 Beamish, 1974
<i>Pimephales promelas</i>	55			85.3		0.07	Webb, 1982
<i>Pimephales promelas</i>	58					<1	Webb, 1986b
<i>Platybio gracilis</i>	170–300 ^b	6.42 \pm TL ^{0.67}				600	12–20 Jones et al., 1974
<i>Protopium williamsi</i>	304 ^b	42.5				600	12–20 Jones et al., 1974
<i>Rhodeus amarus</i>	27–56	24–42 ^c				14	
<i>Rutilus rutilus</i>	120/280	111/122					
<i>Rutilus rutilus</i>	34–62	34–50					
<i>Rutilus rutilus</i>	45–100	91–110					
<i>Rutilus rutilus</i>	6.3–15	–14.06 + 1.38 TL + 0.69 T (cm s^{-1})	13.3–17.2	171.4	32.8	5–6/h	18–22 Pavlov et al., 1972
<i>Rutilus rutilus</i>	6–15		13.3			180	16–18 Zerrath, 1996
<i>Rutilus rutilus</i>	6–43 ^a	–3.64 + 0.5 T + 0.49 SL (cm s^{-1})				180	13–20 Mann and Bass, 1997
<i>Rutilus rutilus caspius</i>	8–30	9–35 ^c				180	19–20 Cowx and Welcomme, 1998
<i>Rutilus rutilus caspius</i>	25–34	28.4–37.3/31.0–46.8				180	8–22 Garner, 1999
<i>Rutilus rutilus caspius</i>	25–44	31–52 ^c				17–21	Pavlov et al., 1972
						17/22	Pavlov et al., 1972
							Pavlov, 1989

Table 1. Continued

Species	Length (mm)	Swimming performance			Time (s)	Temp (°C)	Reference
		U_{crit} cm s^{-1}	U_{crit} FL s^{-1}	U_{max} cm s^{-1}	U_{max} BL s^{-1}		
<i>Salmo salar</i>	750–850			500–600	5.9–8		Hertel, 1966
<i>Salmo salar</i>	25–8	15/19				900	Heggenes and Traaen, 1988
<i>Salmo salar</i>	27–8	17/19/27				900	Heggenes and Traaen, 1988
<i>Salmo salar</i>	600	17/6/21/6				600	Booth et al., 1997
<i>Salmo salar</i>	70 ^b			60 ± 1		300	McDonald et al., 1998
<i>Salmo trutta</i>	130/370			137/305	8.2/10	2	Blaxter and Dickson, 1959
<i>Salmo trutta</i>	250			380	15		Hertel, 1966
<i>Salmo trutta</i>	26–1	15/19/24				900	Heggenes and Traaen, 1988
<i>Salmo trutta</i>	32–1	23/24				900	Heggenes and Traaen, 1988
<i>Salmo trutta</i>	13–22/22–66			13–60/25–100 ^c		<0.2	Hale, 1999
<i>Salvelinus alpinus</i>	355 ^b	100.2				600	Jones et al., 1974
<i>Salvelinus fontinalis</i>	110/116 ^a		6.17/7.65			90/30–15	Petersen, 1974
<i>Salvelinus fontinalis</i>	112 ^a	93	8.3			10	Petersen, 1974
<i>Salvelinus fontinalis</i>	24–2	17/19				900	Heggenes and Traaen, 1988
<i>Salvelinus fontinalis</i>	28 ^b			21.2		2	McLaughlin and Noakes, 1998
<i>Salvelinus fontinalis</i>	70 ^b			46 ± 1		300	McDonald et al., 1998
<i>Salvelinus fontinalis</i>	27–8	13/15/22				900	Heggenes and Traaen, 1988
<i>Salvelinus namaycush</i>	420	191				18	Ohlmer and Schwartzkopf, 1959
<i>Sander lucioperca</i>	130–168 ^b			40–70		<60	Adams et al., 1999a
<i>Scaphirhynchus albus</i>	170–205 ^b			55–70		<60	Adams et al., 1999a
<i>Scardinius erythrophthalmus</i>	120/280	75/94				18	Ohlmer and Schwartzkopf, 1959
<i>Scardinius erythrophthalmus</i>	42–75	36–60 ^c				17–21	Pavlov et al., 1972
<i>Demotilus atrimaculatus</i>	54		8			180	Goolish, 1991
<i>Stenodus leucichthys</i>	80–410 ^b	30.3* FL ^{0.75}				600	Jones et al., 1974
<i>Stizostedion vitreum</i>	8.5/10.5/13.5	1.3/3.2/4.2	1.53/3.05/3.11			1 h	Houde, 1969
<i>Stizostedion vitreum</i>	14.5/15.5	4.6/5.0	3.17/3.23			1 h	Houde, 1969
<i>Stizostedion vitreum</i>	80–380 ^b	13.07* FL ^{0.51}				600	Jones et al., 1974
<i>Thymallus arcticus</i>	70–370 ^b	36.32* FL ^{0.19}				600	Jones et al., 1974
<i>Tinca tinca</i>	255			138	7.5	<1	Komarow, 1971
<i>Tinca tinca</i>	22–69	20–42 ^c					Pavlov, 1989
<i>Umbra limi</i>	53		4.8			180	Goolish, 1991
<i>Vimba vimba</i>	42–69	40–48 ^c					Pavlov, 1989

* Cited in Blaxter (1969); ^a standard length; SL (mm); ^b fork length; FL (mm); ^c estimated from figure; ^d warm adapted (28 °C) carp at 20 °C; ^e largemouth bass conditioned at 0.35 m s⁻¹ for 30 days; ^f anadromous form.

