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

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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} (0.7–1.0 m s^{-1}) accompanied by a 0.1–0.3 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 s – 60 min without fatigue) and 47 mm at burst performance (<20 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 500,000–600,000 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 km of inland waterways, (2) the territory of the former USSR with 144,500 km navigable inland waterways, (3) USA with 41,403 km, and (4) the Far East and China, with more than 155,000 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; Colvile 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; Hüsig 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 Vilcinskas, 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 stess, 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 Vilcinskas, 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 (Jackivicz and Kuzminski, 1973; Liddle and Scorgie, 1980; Holland and Sylvester, 1983; Nielsen et al., 1986; Brookes and Hanbury, 1990; Adams, 1993; Murphy et al., 1995; Wolter and Vilcinskas, 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; Maynord 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; Maynord, 1999; Oebius, 2000b), determine critical tow speeds (e.g. Bhowmik et al., 1995; Sorensen, 1997; Fuehrer and Pagel, 2000; Hüsig et al., 2000), decrease resupension 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. Hüsig and Linke, 1999; Hüsig 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 (Garrad 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 platorynchus*), 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. Hüsig 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 Scorgie, 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 macro-crustaceans 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 (R_e = ratio of inertial over viscous forces) of $R_e < 10$, 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; Drucker, 1996; van Damme and van Dooren, 1999; Drucker 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 Drucker (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 (Drucker, 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 temparatures 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 Russin 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 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 performace 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 performace 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 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.

$U_{burst} = 0.028 * TL^{0.79}$

$R^2 = 0.77$, $p<0.001$

Burst speed (m s^{-1})

Total length (mm)

▾ Acipenseridae
∗ Salmonidae
◆ Esocidae
+ Percidae
□ Cyprinidae
△ Other

$U_{crit} = 0.019 * TL^{0.75}$

$R^2 = 0.69$, $p<0.001$

Critical speed (m s^{-1})

Total length (mm)

▾ Acipenseridae
∗ Salmonidae
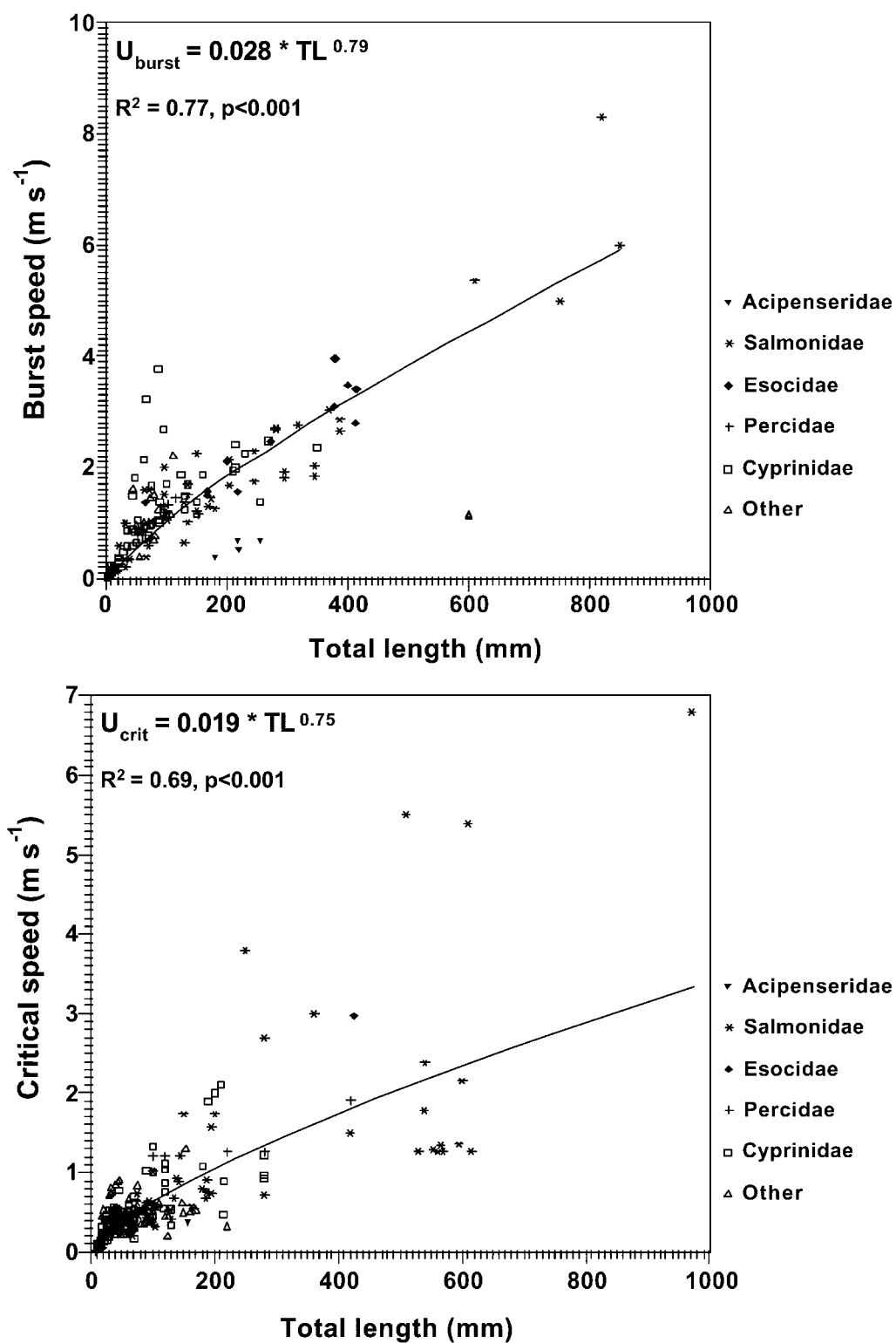◆ Esocidae
+ Percidae
□ Cyprinidae
△ Other

Figure 1. General models of burst speed and critical speed of freshwater fish compiled from various studies (for references compare Table 1).
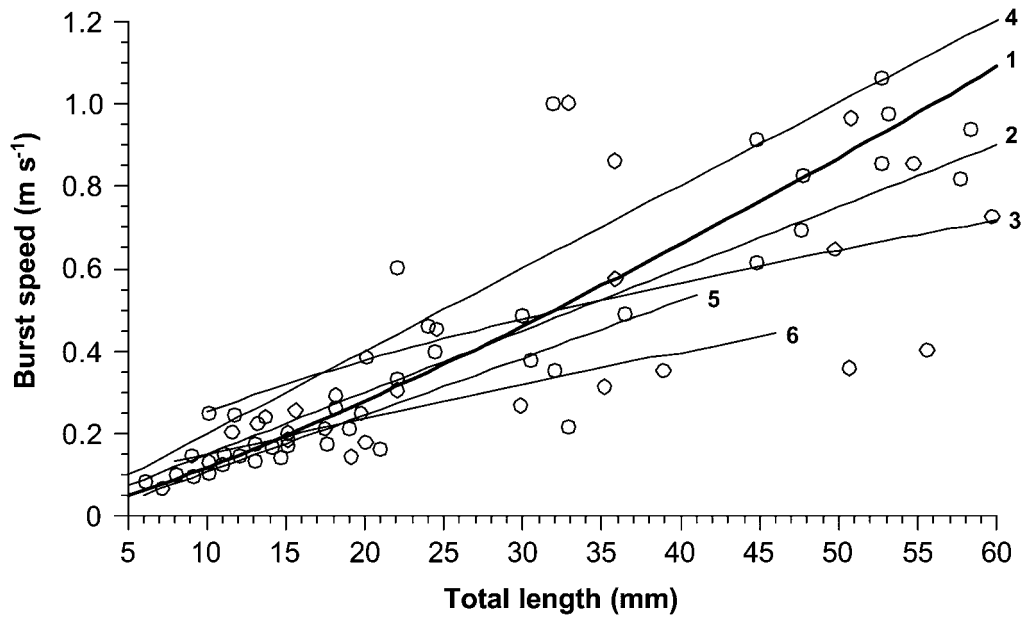
Figure 2. Size-dependent burst performance of small fish up to 60 mm total length compiled from Table 1. Numbers refer to burst speeds according to (1) own model $U_{burst} = 0.0068 * TL^{1.24}$, $R^2 = 0.83$, $p < 0.001$; (2) Wardle (1975); (3) Wakeling et al. (1999) for carp; (4) Flore et al. (2001) 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; Hüsig 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; Maynord 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; Maynord, 1999; Fuehrer and Pagel, 2000), drawdowns between 0.10–0.95 m (Soong and Bhowmik, 1992; Jähne et al., 1993; Maynord and Martin, 1997; Fuehrer, 1998; Maynord, 1999; Fuehrer and Pagel, 2000; Heibaum and Soyeaux, 2002), return currents between 0.4–1.1 m s^{-1} (Maynord and Martin, 1997; Fuehrer, 1998; Maynord, 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/publikations.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 freqency, navigation-induced disturbances differ significantly from comparable hydraulic impacts from hydropower stations. Although especially propeller-typed turbines of power-generatig 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
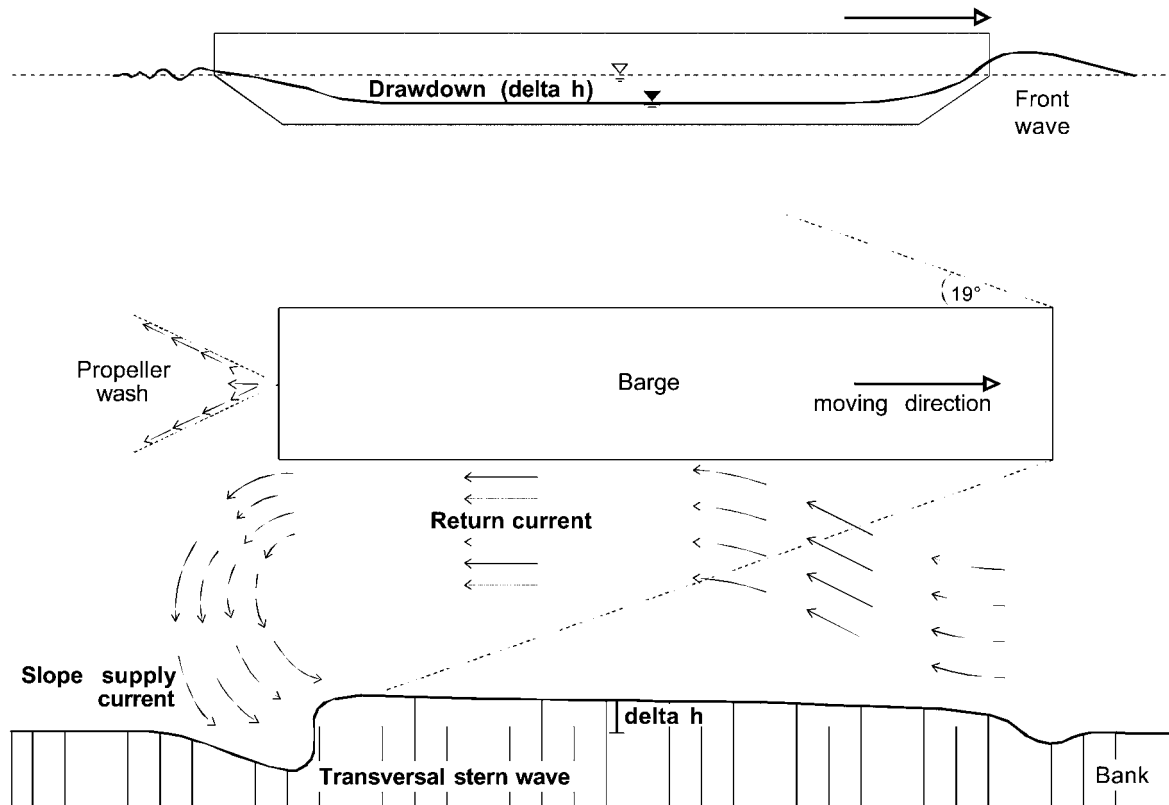
Figure 3. Navigation-induced physical forces in restricted waterways (modified from Bhowmik and Mazumder, 1990; Fuehrer, 1998; Oebius, 2000b).

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 (Hüsig 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 (Hüsig et al., 2000) which is well within the subcritical mode (Fuehrer, 1998; Hüsig and Linke, 1999; Fuehrer and Pagel, 2000; Hüsig et al., 2000; Maynord, 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 80–90% V_{crit}, the navigation-induced return currents along the shore were usually around 0.8 m s^{-1} accompanied by a 0.1–0.3 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 mm total length (Figure 2) and of critical performance (>20 s to 1 h without fatigue) for fish <147 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, exept pelagophils and litho-pelagophils, have their first nursery habitats in
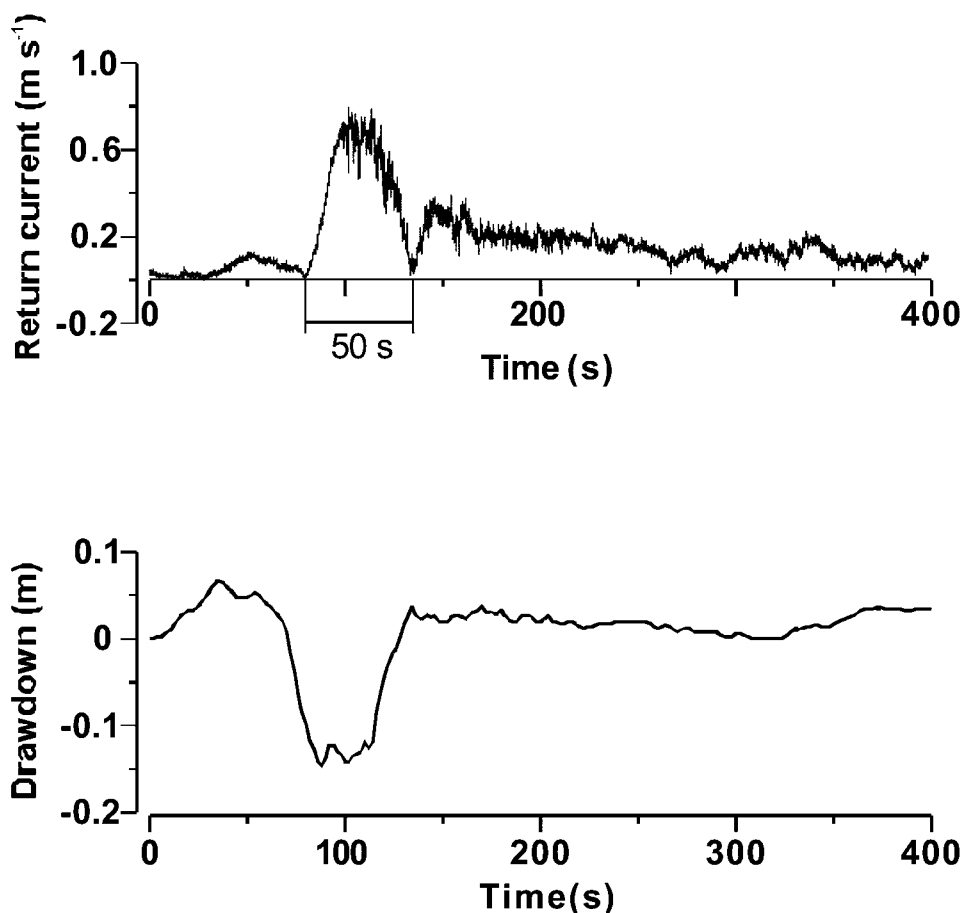
Figure 4. Typical return current patterns and dynamic water level sinkage measured during the passage of a 81.5 m barge tow at 8.0 km h^{-1} and an A_s:A_c ratio of 0.14 in a German waterway (data source Arlinghaus et al., 2002b).

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; Maynord, 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 m s^{-1} (e.g. Fuehrer, 1998; Maynord, 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 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 Vilcinskas (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 Vilcinskas, 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 Vilcinskas, 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 Vilcinskas, 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 (0.6–0.8 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 0.6–1 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; Maynord, 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; Maynord, 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 emmissions could be improved to be sustainable as well in regard to maintain aquatic organisms.

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Appendix

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

Species	Length (mm)	Swimming performance U_crit cm s⁻¹	U_crit BL s⁻¹	U_max cm s⁻¹	U_max BL s⁻¹	Time (s)	Temp (°C)	Reference
Abramis ballerus	17–59	22–51^c						Pavlov, 1989
Abramis bjoerkna	22			30	15			Radakov, 1964*
Abramis brama	120/280	87/96					18	Ohlmer and Schwartzkopff, 1959
Acipenser fulvescens	157	38.6	2.45			120	15	Webb, 1986a
Acipenser gueldenstaedti	40–69	22–29^c					18–22	Pavlov et al., 1972
Acipenser stellatus	55–70	21–26^c					18–22	Pavlov et al., 1972
Alburnoides bipunctatus	33–60		10.1			180	15–16	Cowx and Welcomme, 1998
Alburnus alburnus	19–34	31–53^c						Pavlov, 1989
Anguilla anguilla	600			114	1.9	2	10	Blaxter and Dickson, 1959
Anguilla anguilla	72	54	7.5			18	11–13	McCleave, 1980
Anguilla anguilla	170–450	−0.82 + 0.45 ln (TL)				120–180	17	Sprengel and Lüchtenberg, 1991
Anguilla anguilla	220	31.8	1.58				18–22	D'Aoûts and Aerts, 1999
Anguilla rostrata	56	30		40			17–23	Barbin and Krueger, 1994
Barbatula barbatula	91	53.0/60.8	5.6/5.8		14.2	600	4/20	Stahlberg, 1986
Barbatula barbatula	110	60.8	5.5			180	18	Stahlberg and Peckmann, 1987
Barbatula barbatula	22–42	22.5–38^c					18–22	Pavlov et al., 1972
Barbus barbus	19–30		11.5			180	15–16	Cowx and Welcomme, 1998
Carassius auratus	90			138	15.1	2	10	Blaxter and Dickson, 1959
Carassius auratus	67–213	42–48	6.3–3.8	74–200	11–9.4	1/20	14	Bainbridge, 1960
Carassius auratus	50–210		10				15	Blaxter, 1969
Carassius auratus	180			108	8		13	Hertel, 1966
Carassius carassius	100				11.4	6	13	Tsukamoto et al., 1975
Carassius carassius	18–42	20–49^c						Pavlov, 1989
Carassius gibelio	230			226	9.8	<1		Komarow, 1971
Catostomus catostomus	40–530^b	11.03*FL$^{0.53}$				600	12–20	Jones et al., 1974
Catostomus commersoni	170–370^b	10.03*FL$^{0.55}$				600	12–20	Jones et al., 1974
Chalcalburnus chalcoides	125			187	15	<1		Komarow, 1971
Chalcalburnus chalcoides	9/13/17	6.3/7.3/8.7					15	Wieser and Kaufmann, 1998
Chalcalburnus chalcoides	9/13/17	7.8/10/11.6					20	Wieser and Kaufmann, 1998
Chondrostoma nasus	15–45	4.39 + 0.456 TL (cm s⁻¹)					16	Flore et al., 2001
Cobitis taenia	34–71	25–42^c						Pavlov, 1989
Coregonus autumnalis	421^b	80				600	12–20	Jones et al., 1974
Coregonus clupeaformis	60–510^b	18.2*FL$^{0.35}$				600	12–20	Jones et al., 1974

Table 1. Continued

Species	Length (mm)	Swimming performance U_{crit} cm s⁻¹	U_{crit} BL s⁻¹	U_{max} cm s⁻¹	U_{max} BL s⁻¹	Time (s)	Temp (°C)	Reference
Coregonus nasus	60–330[b]	9.7*FL^0.45				600	12–20	Jones et al., 1974
Coregonus sardinella	295[b]	60				600	12–20	Jones et al., 1974
Cottus cognatus	82				9.4	0.081	15	Webb, 1978
Cottus gobio	16–41	15–34[c]						Pavlov, 1989
Cyprinus carpio	350			236	8.2	<1		Komarow, 1971
Cyprinus carpio	70–130		2.43/2.63		4.1[d]		10/20	Heap and Goldspink, 1986
Cyprinus carpio	36–77	86–98	13.6–15.6	166.4	26.7	3–4.5/1	16–18	Zerrath, 1996
Cyprinus carpio	10–62.5			3.71*TL^0.584 (m s⁻¹); TL in m		<0.5	20–21	Wakeling et al., 1999
Danio rerio	3.6			1.8–2.4	50–66	<1	21–30	Fuiman, 1986
Danio rerio	31.8–39.7[a]	56 ± 4.8	15.5[a]			300	28	Plaut, 2000
Esox lucius	425	297					18	Ohlmer and Schwartzkopff, 1959
Esox lucius	170–200			150–210	7.5–12.5			Hertel, 1966
Esox lucius	120–620[b]	4.9*FL^0.55	600				12–20	Jones et al., 1974
Esox lucius	217				7.2	0.115	15	Webb, 1978
Esox lucius	380			397	8.2–10.5	0.1–0.2		Harper and Blake, 1991
Esox lucius	412[b]			280/340		0.13/0.16	8–12	Frith and Blake, 1995
Etheostoma caeruleum	62				14.4	0.056	15	Webb, 1978
Gasterosteus aculeatus	44.4[a]	108		159		0.05	15	Law and Blake, 1996
Gasterosteus aculeatus	60	66.1	11.1					Taylor and MacPhail, 1986
Gasterosteus aculeatus	55	36.3	6.6			180	18	Stahlberg and Peckmann, 1987
Gasterosteus aculeatus	50	35	7			60	20	Whoriskey and Wootton, 1987
Gasterosteus aculeatus	33–74	80–83	15.8–16.6	145	33.5	4.5–5/1	16–18	Zerrath, 1996
Gobio gobio	61–80	31–37/43–51				180	3/20	Pavlov et al., 1972
Gobio gobio	116	43.0/55.0	3.64/4.66		19.7	600	4/20	Stahlberg, 1986
Gobio gobio	118	45.6/55.0	3.9/4.7			180	4/18	Stahlberg and Peckmann, 1987
Gobio gobio	53–95	106–119	15–16.7	268	36.2	5/1	16–18	Zerrath, 1996
Gobio gobio	28–50		8.85			180	15–16	Cowx and Welcomme, 1998
Gymnocephalus cernuus	105			133	12.7	<1		Komarow, 1971
Hiodon alosoides	225[b]	60				600	12–20	Jones et al., 1974
Huso huso	52–70	21–29[c]						Pavlov, 1989
Hypophthalmichthys molitrix	270			248	9.2	<1		Komarow, 1971
Leponis cyanellus	80				8.4	0.079	15	Webb, 1975b
Leponis cyanellus	80			150	18.8	0.08		Beamish, 1978
Leponis macrochirus	153				8.5	0.088	15	Webb, 1978
Leponis macrochirus	64				15.8	<1	15	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}	U_{max} BL s^{-1}			
Leucaspius delineatus	30–41	36–55[c]					18–22	Pavlov et al., 1972
Leucaspius delineatus	51	22.7/38.6	4.5/7.7			180	4/18	Stahlberg and Peckmann, 1987
Leuciscus cephalus	48–64	82–92	15.2–17	214.5	37.7	4–6/1	16–18	Zerrath, 1996
Leuciscus cephalus	66–87	96–106	12.5–13.7	376.2	49	4–6/1	16–18	Zerrath, 1996
Leuciscus cephalus	6–43[a]	0.45 + 0.23 T + 0.55 SL (cm s^{-1})				180	8–22	Garner, 1999
Leuciscus leuciscus	100–214	46–90	4.4–4.2	110–240	11.2–11	1/20	14	Bainbridge, 1960
Leuciscus leuciscus	8.3–17.3	−19.39 + 1.46 TL + 0.9 T (cm s^{-1})				180	13–20	Mann and Bass, 1997
Leuciscus leuciscus	9–25		10.3			180	15–16	Cowx and Welcomme, 1998
Leuciscus leuciscus	6–43[a]	−7.4 + 1.0 T + 0.83 SL (cm s^{-1})				180	8–22	Garner, 1999
Lota lota	120–620[b]	30.6*FL$^{0.07}$				600	12–20	Jones et al., 1974
Micropterus salmoides	102[b]	50[c]	5[c]			300	25	Farlinger and Beamish, 1977
Micropterus salmoides	142[b]	47.7[e]				1800	25	Farlinger and Beamish, 1978
Micropterus salmoides	51				18.8	<1	15	Webb, 1986b
Micropterus salmoides	93–128[b]		2.22/2.9[c]/3.6[c]			1200	5/10/17	Kolok, 1991
Notropis atherinoides	65[a]	59				600	12–20	Jones et al., 1974
Notropis cornutus	107				10.7	0.078	15	Webb, 1978
Oncorhynchus clarki	87–100[b]		5.58			900	10	Hawkins and Quinn, 1996
Oncorhynchus kisutch	360–610	300–540	6–9					Weaver, 1963*
Oncorhynchus kisutch	64.3		5.63			1 h	13	Howard, 1975
Oncorhynchus kisutch	40–60[b]		3.5/7.3	40		1 h	3/23	Glova and McInerney, 1977
Oncorhynchus kisutch	80–120[b]		3.5/5.5	65		1 h	3/23	Glova and McInerney, 1977
Oncorhynchus kisutch	55[a]	62.9–74.1		102.3–104.7			13.5	Taylor and McPhail, 1985
Oncorhynchus kisutch	19–32			14–100[c]		<0.2	12	Hale, 1999
Oncorhynchus kisutch	32–72			35–160[c]		<0.2	12	Hale, 1999
Oncorhynchus mykiss	103–280			105–270/32–73	10.2–7.6/3.1–2.6	1/20	14	Bainbridge, 1960
Oncorhynchus mykiss	610–820	430–830	7–13					Weaver, 1963*
Oncorhynchus mykiss	48/358[b,d]		9/5.5			60	10	Fry and Cox, 1970
Oncorhynchus mykiss	305.8[b]	66.57				600	12–20	Jones et al., 1974
Oncorhynchus mykiss	143				8.5	0.078	15	Webb, 1975b
Oncorhynchus mykiss	96/150/204			202/226/214	21/15/10.5	<1	15	Webb, 1976
Oncorhynchus mykiss	245–387	229–265			9.3–6.8	<1	15	Webb, 1976
Oncorhynchus mykiss	195				8.1	0.114	15	Webb, 1978
Oncorhynchus mykiss	318				8.7	0.125	15–20	Harper and Blake, 1990
Oncorhynchus mykiss	95				13.7	0.074	10	Gamperl 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}			
Oncorhynchus mykiss	87–100[b]		7.69			900	10	Hawkins and Quinn, 1996
Oncorhynchus mykiss	87[b]		6			180/220	15	Gregory and Wood, 1998
Oncorhynchus nerka	162	58	3.65			1200	10	Brett, 1964
Oncorhynchus nerka	188	76.9	4.12			1200	15	Brett, 1964
Oncorhynchus nerka	195	74.1	3.9			1200	20	Brett, 1964
Oncorhynchus nerka	77–128	51.5–59.8	4.2–6.7			1 h	15	Brett and Glass, 1973
Oncorhynchus nerka	56–98	37.1–64.4	8.2–5.9			1 h	20	Brett and Glass, 1973
Oncorhynchus nerka	530–614	127–136	2.1–2.4			1 h	20	Brett and Glass, 1973
Oncorhynchus nerka	77.7[b]	53.3/60.1[f]	7.3/8.3[f]			1200	10	Taylor and Foote, 1991
Oncorhynchus tshawytscha	510–970	550–680	7–11					Weaver, 1963*
Oncorhynchus tshawytscha	21–33/39–65			16–100/35–160[c]		<0.2	12	Hale, 1999
Osmerus eperlanus	50–170	$-0.16 + 0.24 \ln (TL)$				120–180	17	Sprengel and Lüchtenberg, 1991
Perca flavescens	7.5/10.5/13.5	1.4/3.2/4.6	1.87/3.05/3.41			1 h	13	Houde, 1969
Perca flavescens	100[a]	33.5				900	20	Otto and O'Hara Rice, 1974
Perca flavescens	155				7.4		15	Webb, 1978
Perca fluviatilis	100/220	121/126				0.103	18	Ohlmer and Schwartzkopff, 1959
Perca fluviatilis	115			145	12.6	<1		Komarow, 1971
Perca fluviatilis	46–64	56–60[c]					18–22	Pavlov et al., 1972
Perca fluviatilis	72[b]	55				600	12–20	Jones et al., 1974
Percopsis omiscomaycus	123–148	20–60				600	12–20	Jones et al., 1974
Petromyzon marinus	55					1800	5–15	Beamish, 1974
Pimephales promelas	55			85.3		0.07	15	Webb, 1982
Pimephales promelas	58				14	<1	15	Webb, 1986b
Platygobio gracilis	170–300[b]	$6.42 \ast FL^{0.67}$				600	12–20	Jones et al., 1974
Prosopium williamsoni	304[b]	42.5				600	12–20	Jones et al., 1974
Rhodeus amarus	27–56	24–42[c]						Pavlov, 1989
Rutilus rutilus	120/280	111/122					18	Ohlmer and Schwartzkopff, 1959
Rutilus rutilus	34–62	34–50					18–22	Pavlov et al., 1972
Rutilus rutilus	45–100	91–110	13.3–17.2	171.4	32.8	5–6/1	16–18	Zerrath, 1996
Rutilus rutilus	6.3–15	$-14.06 + 1.38\,TL + 0.69\,T$ (cm s^{-1})				180	13–20	Mann and Bass, 1997
Rutilus rutilus	6–15	13.3				180	19–20	Cowx and Welcomme, 1998
Rutilus rutilus	6–43[a]	$-3.64 + 0.5\,T + 0.49\,SL$ (cm s^{-1})				180	8–22	Garner, 1999
Rutilus rutilus caspius	8–30	9–35[c]					17–21	Pavlov et al., 1972
Rutilus rutilus caspius	25–34	28.4–37.3/31.0–46.8					17/22	Pavlov et al., 1972
Rutilus rutilus caspius	25–44	31–52[c]						Pavlov, 1989

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}			
Salmo salar	750–850			500–600	5.9–8			Hertel, 1966
Salmo salar	25.8	15/19				900	6/14	Heggenes and Traaen, 1988
Salmo salar	27.8	17/19/27				900	7/8/18	Heggenes and Traaen, 1988
Salmo salar	600	176/216				600	12/18	Booth et al., 1997
Salmo salar	70[b]			60±1		300	11–13	McDonald et al., 1998
Salmo trutta	130/370			137/305	8.2/10	2	10	Blaxter and Dickson, 1959
Salmo trutta	250			380	15			Hertel, 1966
Salmo trutta	26.1	15/19/24				900	6/14/19	Heggenes and Traaen, 1988
Salmo trutta	32.1	23/24				900	7/18	Heggenes and Traaen, 1988
Salmo trutta	13–22/22–66			13–60/25–100[c]		<0.2	12	Hale, 1999
Salvelinus alpinus	355[b]	100.2				600	12–20	Jones et al., 1974
Salvelinus fontinalis	110/116[a]		6.17/7.65			90/30	15	Petersen, 1974
Salvelinus fontinalis	112[a]	93	8.3			10	15	Petersen, 1974
Salvelinus fontinalis	24.2	17/19				900	6/14	Heggenes and Traaen, 1988
Salvelinus fontinalis	28[b]			21.2		2		McLaughlin and Noakes, 1998
Salvelinus fontinalis	70[b]			46 ± 1		300	11–13	McDonald et al., 1998
Salvelinus namaycush	27.8	13/15/22				900	6/14/19	Heggenes and Traaen, 1988
Sander lucioperca	420	191					18	Ohlmer and Schwartzkopff, 1959
Scaphirhynchus albus	130–168[b]			40–70		<60	17–20	Adams et al., 1999a
Scaphirhynchus albus	170–205[b]			55–70		<60	17–20	Adams et al., 1999a
Scardinius erythrophthalmus	120/280	75/94					18	Ohlmer and Schwartzkopff, 1959
Scardinius erythrophthalmus	42–75	36–60[c]					17–21	Pavlov et al., 1972
Semotilus atromaculatus	54		8			180	22	Goolish, 1991
Stenodus leucichthys	80–410[b]	$30.3*FL^{0.75}$				600	12–20	Jones et al., 1974
Stizostedion vitreum	8.5/10.5/13.5	1.3/3.2/4.2	1.53/3.05/3.11			1 h	13	Houde, 1969
Stizostedion vitreum	14.5/15.5	4.6/5.0	3.17/3.23			1 h	13	Houde, 1969
Stizostedion vitreum	80–380[b]	$13.07*FL^{0.51}$				600	12–20	Jones et al., 1974
Thymallus arcticus	70–370[b]	$36.32*FL^{0.19}$				600	12–20	Jones et al., 1974
Tinca tinca	255			138	7.5	<1		Komarow, 1971
Tinca tinca	22–69	20–42[c]						Pavlov, 1989
Umbra limi	53		4.8			180	22	Goolish, 1991
Vimba vimba	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.