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Leibniz-Institut für Gewässerökologie und Binnenfischerei
Leibniz-Institute of Freshwater Ecology and Inland Fisheries
im Forschungsverbund Berlin e.V.

3.2.2 **Burst and critical swimming speeds of fish and their ecological relevance in waterways**

Maximale und kritische Schwimgeschwindigkeiten von Fischen und ihre ökologische Relevanz in Wasserstraßen

Keywords: navigation, fish larvae, hydraulic forces, habitat bottleneck hypothesis

Abstract

A total of 168 swimming performance studies for 75 freshwater fish species were compiled with the aim of characterising the absolute swimming performance of fish as a prerequisite (1) to spatially analyse distribution pattern, age and size structure of fish assemblages in river systems, and (2) to predict impacts on fish resulting from human alterations of hydrodynamics. It was hypothesized that swimming performance is a crucial factor for the habitat use in freshwater ecosystems characterized by pulsed perturbations or unsteady flows resulting from navigation or related hydrodynamic impacts. Models regressing total length on burst and critical swimming speeds were highly significant. According to these models, a swimming speed of 1.0 m s^{-1} will be maintained by a 56 mm long fish in the burst mode (maximum duration until fatigue 20 s). No significant differences in burst swimming performance were detected between small-sized individuals of cyprinids, salmonids and other taxonomic orders. In the critical swimming mode (up to 1 h until fatigue), the same speed (1.0 m s^{-1}) will be reached by a 133 mm long cyprinid, a 179 mm fish in general, or a 201 mm salmonid fish. In this prolonged mode, rheophilic cyprinids performed significantly better than salmonids or other fish.

In restricted inland waterways, moving vessels typically induce return currents of $0.7\text{-}1.1 \text{ m s}^{-1}$ and dynamic flow patterns acting along the shoreline. The gap between the maximum swimming ability of newly hatched fish ranging between $0.06\text{-}0.2 \text{ m s}^{-1}$, and the navigation-induced physical threshold (0.7 m s^{-1}) maintained by a 42 mm long fish in the burst mode and by a 71 mm long fish in the critical mode, led to the inference of the navigation-induced habitat bottleneck hypothesis (NBH). According to the NBH, the restricted availability of essential nurseries for early fish life stages resulting from their limited swimming performance is the major bottleneck for fish recruitment in waterways. The models of burst and critical swimming speed introduced here can help to establish appropriate management options aiming at sustaining fish biodiversity in highly modified water bodies.

Zusammenfassung

Ein-hundertachtund-sechzig Untersuchungen zur Schwimmleistung von insgesamt 75 Süßwasserfischarten wurden analysiert, um die absolute Schwimmleistung von Fischen als elementaren Faktor der Habitatnutzung in

störungsdominierten Lebensräumen mit hochvariablen Strömungen zu charakterisieren. Die modellgestützte Ableitung der Schwimmleistung von Fischen dient (1) der räumlichen Analyse von Verteilungsmustern, Alters- und Größenstruktur von Fischgemeinschaften sowie (2) der Prognose von Beeinträchtigungen der Fische als Folge menschlicher Einflussnahme auf die hydrodynamischen Verhältnisse.

Regressionsmodelle der Gesamtkörperlänge zur Sprint- und kritischen Schwimgeschwindigkeit erwiesen sich als höchst signifikant, wonach eine Schwimgeschwindigkeit von $1,0 \text{ m s}^{-1}$ der Sprintleistung (maximal 20 s bis zur Erschöpfung) eines 56 mm langen Fisches entspricht. Bei kleinen Fischen bis 60 mm Körperlänge wurden beim Vergleich von Cypriniden, Salmoniden und anderen taxonomischen Gruppen keine signifikanten Unterschiede der Sprintleistung festgestellt. Die gleiche Geschwindigkeit ($1,0 \text{ m s}^{-1}$) im kritischen Leistungsbereich (eine Stunde bis zur Erschöpfung) erreichen 133 mm lange Cypriniden oder 201 mm lange Salmoniden, bzw. dem allgemeinen Modell entsprechend, ein 179 mm langer Fisch. Die Ausdauerleistung der rheophilen Cypriniden übertraf signifikant die der Salmoniden oder anderer taxonomischer Gruppen.

Im begrenzten Fahrwasser der Binnenwasserstraßen erzeugen fahrende Schiffe typischerweise Rückströmungen von $0,7\text{-}1,1 \text{ m s}^{-1}$ und sehr dynamische Strömungsmuster entlang des Ufers. Die Differenz zwischen diesen Schifffahrts-induzierten physikalischen Schwellenwerten – $0,7 \text{ m s}^{-1}$ entsprechen der Sprint- und kritischen Schwimmleistung eines 42 mm bzw. 71 mm langen Fisches – und der maximalen Schwimmleistung eines frisch geschlüpften Jungfisches ($0,06\text{-}0,2 \text{ m s}^{-1}$) führten zur Ableitung der Navigations-induzierten „habitat bottleneck hypothesis“ (NBH). Gemäß dieser Hypothese ist die aufgrund ihrer begrenzten Schwimmleistung eingeschränkte Verfügbarkeit der für Jungfische essentiellen Brutaufwuchshabitate der Haupt-Engpass für die Rekrutierung der Fische in Wasserstraßen. Die Modelle zur Schwimmleistung von Fischen erlauben die Ableitung von konkreten Managementempfehlungen zum Erhalt der Fischartendiversität in Wasserstraßen.

3.2.2.1 Introduction

Locomotion is the behaviour that most dictates the morphology and physiology of animals. Evolutionary pressures for efficient, functional, rapid, or reliable movements often shape organism design (Dickinson et al. 2000, Liao et al. 2003, Taylor et al. 2003, Donley et al. 2004). For example, although lamnid sharks (Family Lamnidae) and tunas (Family Scombridae) independently evolved a mode of living in the open sea requiring continuous swimming and short-duration high-speed swimming, the strong selective influence of hydromechanics resulted in similar morphologies (Bernal et al. 2001, Donley et al. 2004).

Swimming performance is one of the crucial factors determining the survival of most fish species within the aquatic environment. Not surprisingly, large variations in swimming ability exist among the highly diverse group of teleosts. For example, the sailfish (*Isitiophorus platypterus*) is often considered

as the fastest fish of the world with an observed maximum speed of 30 m s^{-1} (Johnson & Gill 1998), and maximum speeds of 20.8 m s^{-1} and 21.4 m s^{-1} were measured for a 0.98 m long yellowfin tuna (*Thunnus albacares*) and a 1.13 m long wahoo (*Acanthocybium solandri*) respectively (Walters & Fierstine 1964), while anglerfish males of the Family Ceratiidae experience complete atrophy of their axial musculature and become parasitic appendages of the female (Pietsch 1976). Many fish species have evolved specialist locomotor strategies, often at the expense of another type of locomotion (Webb 1984). According to their morphology, tuna, pike (genus *Esox*) and banded butterfly fish (genus *Chaetodon*) are specialized for one swimming function, namely sustained cruising, accelerating in quick strikes at prey and low-speed maneuvering in and around coral reefs respectively (Webb 1984). Each specialist performs poorly in the other two types of locomotion. In contrast, for example, surf perch of the genus *Rhacochilus* are generalists. They cruise, accelerate and maneuver fairly well, but do not perform any function as well as a specialized species (Webb 1984).

Predator-prey interactions, reproductive behaviour (in particular spawning migrations), habitat shifts, dispersal and habitat maintenance in hydrodynamically determined environments are of profound ecological importance and depend substantially on the individuals' capacity for locomotion (Kolok 1999, Reidy et al. 2000, Plaut 2001). Maximum speed, acceleration, and endurance of swimming are directly related to food capture, escape from predators, and thus, finally, to survival. Therefore, logic dictates that swimming performance is subjected to a strong selection pressure and factors into Darwinian fitness of fish (Beamish 1978, Videler & Wardle 1991, Videler 1993, Johnson & Bennett 1995, Reidy et al. 2000, Domenici 2001), which is related to the observed significant intra-specific variability of individuals' locomotor performance (Kolok 1999, Reidy et al. 2000, Boily & Magnan 2002).

However, swimming performance has not only its evolutionary dimensions, but is also highly relevant in an ecological context. The present study focuses on the swimming performance of fish as a crucial factor for maintaining its position in unsteady flows, which are particularly pronounced in navigable waterways. Models of critical and burst swimming performance were derived, serving as a prerequisite (1) to spatially analyse distribution pattern, age and size structure of fish assemblages in river systems, and (2) to predict impacts on fish resulting from human alterations of hydrodynamics.

3.2.2.2 Swimming performance

The swimming performance of fish is characterized by the relationship between swimming speed and time until fatigue, and was classified by Webb (1975) 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 critical speed as a special category of prolonged speed: a velocity which could be maintained by a fish 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 & Blake 1997, Reidy et al. 2000), while bursts longer than approximately 2 s will be markedly slower (Hammer 1995).

Swimming performance depends on numerous biological and physical factors (Webb 1975, Webb & Weihs 1983, Videler 1993, Dickinson et al. 2000). Firstly, it is species-specific determined by body shape (Webb 1984, Vogel 1994, Müller et al. 2001, Boily & Magnan 2002), fin form (Webb 1984, Videler 1993, Plaut 2000), muscle function (Webb & Weihs 1983, Rome et al. 1988, Altringham & Ellerby 1999, Kieffer 2000), and swimming mode (Webb & Weihs 1983, Webb 1984, Sfakiotakis et al. 1999, Müller et al. 2001, Liao et al. 2003, Taylor et al. 2003). Secondly, absolute swimming speed increases with fish size (e.g. Wardle 1975, Beamish 1978, Videler 1993, Hammer 1995, Domenici 2001, Wolter & Arlinghaus 2003). Thirdly, in ectotherms, the swimming performance is temperature-dependent (e.g. Wardle 1980, Keen & Farrell 1994, Johnson & Bennett 1995, Taylor et al. 1996, Temple & Johnston 1998, Wieser & Kaufmann 1998, Ojanguren & Braña 2000, Wakeling et al. 2000), although for small fish larvae, viscosity effects are over 10 times more powerful than the temperature effects not linked to viscosity (Fuiman & Batty 1997). Fish larvae hatch in a viscous flow regime, and in particular during their first days of life, viscosity effects are of considerable importance for the energetic costs of swimming (Blaxter 1986, Osse & Drost 1989, Kaufmann 1990, Müller & Videler 1996, Wieser & Kaufmann 1998, McFarlane & McDonald 2002). 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 & Weihs 1986, Hale 1999).

Additional environmental factors influencing the swimming performance of individual fish have been reviewed by Randall & Brauner (1991), Videler (1993), and Hammer (1995), and include pH (Butler et al. 1992, Day & Butler 1996), oxygen tension (Kaufmann 1990, Kaufmann & Wieser 1992, Kieffer 2000, Reidy et al. 2000, Peake & Farrell 2004), photoperiod (Kolok 1991), salinity (Randall & Brauner 1991), and various pollutants (Hammer 1995, Shingles et al. 2001).

Different experimental designs have been used to determine fish swimming speeds (Videler & Wardle 1991, Drucker 1996, van Damme & van Dooren 1999, Kieffer 2000, Plaut 2001), and a scientific debate emerged whether or not per unit body length speed (van Damme & van Dooren 1999) is more ecological relevant than absolute speed (Drucker 1996). With regard to hydrodynamics, particularly under conditions faced in most navigable waterways, absolute swimming performance was considered as

ecologically relevant, because the hydrodynamic characters of the habitat represent physical thresholds determining minimum swimming requirements for habitat use in order to avoid displacement due to navigation-induced currents. Therefore, the absolute swimming speed of fish has been reviewed (Wolter & Arlinghaus 2003) and selected results will be presented below.

Burst and critical swimming speeds

A total of 168 experimental swimming performance studies produced comparable results for 75 freshwater fish species potentially inhabiting waterways in the temperate zone (listed in Wolter & Arlinghaus 2003). Despite of some methodical differences, these studies were used to compute burst and critical swimming speeds in relation to fish size. All findings in a temperature range between 10-20°C have been selected and standardized to total length (TL, mm) and absolute speed (U, m s⁻¹). These results were pre-classified in two groups, burst performance with a duration <20 s, and critical performance (up to 1 h), and analysed separately (details in Wolter & Arlinghaus 2003). A power model fitted best, and was used for regressions of total length and swimming speeds.

Wolter & Arlinghaus (2003) developed a general regression model for burst performance (U_{burst}) depending on total length for fish up to 1 m TL ($R^2 = 0.77$, $p < 0.001$). Accordingly, a 10 cm long fish would perform at more than 1 m s⁻¹. Even in navigable waterways, at shoreline habitats, a flow velocity of 1 m s⁻¹ will rarely be reached (Arlinghaus et al. 2002), and correspondingly, fish able to swim 1 m s⁻¹ or faster should not be affected or limited at all. The performance regressions were recalculated using exclusively studies of fish up to 60 mm TL for burst performance and up to 200 mm TL for critical performance which is generally lower.

Calculated for specimens up to 60 mm TL, the model revealed a significantly (F-test, $p < 0.05$) steeper slope of the regression curve, corresponding with the higher relative (in body length) swimming performance of small fish. Consequently, speeds of 1.0 m s⁻¹ would already be maintained by a 56 mm long fish for 20 s (Figure 1). The general model fitted 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. As expected, salmonids exhibited the highest burst swimming performance, however, the differences detected between the small-sized individuals of different taxonomic orders were not significant (Figure 1, F-test, $p = 0.142$). Thus, the threshold of swimming performance shown in Figure 1 applies for all fish smaller than 60 mm TL, which is important, as one would intuitively think that rheophilic fish perform superiorly to eurytopic and limnophilic fish.

Haefner & Bowen (2002) suggested only the absolute burst swimming performance is a limiting factor for fish to successfully maintain position in current, and derived this conclusion from a modelling approach to evaluate the functioning of a power plant fish collection gallery. However, physical forces often last for more than 20 s, as commonly occurs during hydrodynamic alterations from flush flows, hydropeaking, or when barges

pass. In the critical mode, the 56 mm long, “general” fish mentioned above would perform only 0.54 m s^{-1} (Figure 2).

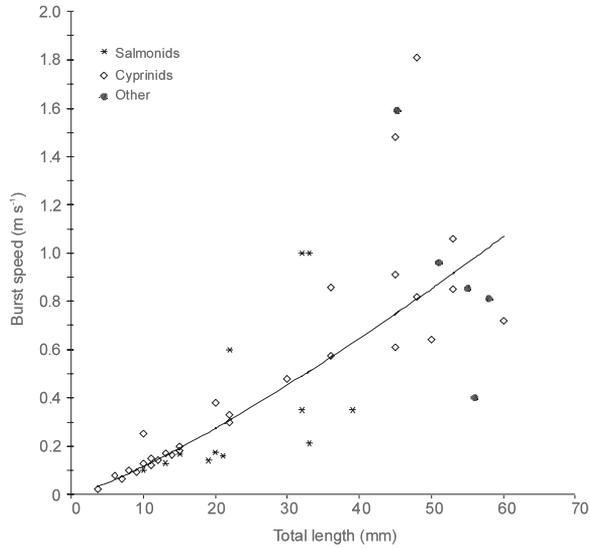


Fig. 1: Burst swimming performance of pooled salmonids, cyprinids, and other fish species up to 60 mm total length (TL) $U_{burst} = 0.0068 * TL^{1.24}$ (d.f. = 84; $R^2 = 0.83$; $p < 0.001$) (modified from Wolter & Arlinghaus 2003).

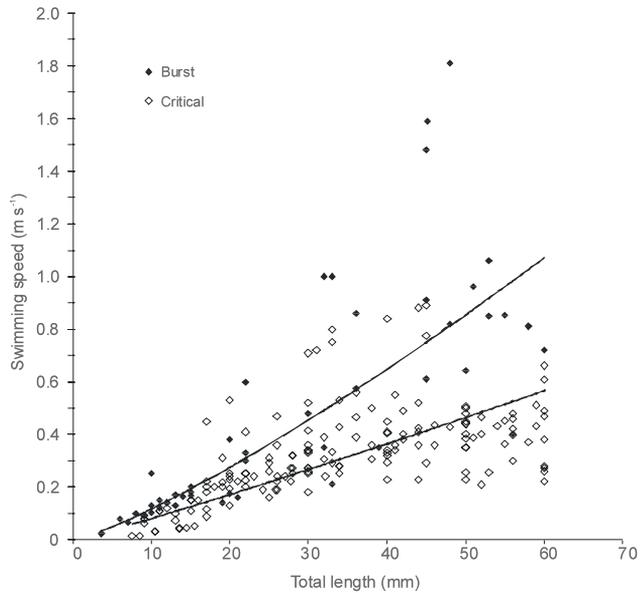


Fig. 2: Comparison of burst and critical swimming performance ($U_{crit} = 0.0067 * TL^{1.09}$; d.f. = 155; $R^2 = 0.60$; $p < 0.001$) of small fish up to 60 mm total length (TL).

Consequently, with regard to hydrodynamic disturbances, the burst performance tends to underestimate an impact, because the maximum swimming speed drops rapidly down after 2-3 s (Hammer 1995), and declines further within the 20th range of burst performance (Wardle 1975, Videler 1993), while the critical speed (maintained per definition up to one hour) is substantially lower than an “uppermost critical” speed which can be maintained for 2-3 min until fatigue only (e.g. Videler 1993, Hammer 1995). Thus, the critical performance tends to overestimate hydrodynamic impacts. The resulting function between both lines in Figure 2 may be an useful approximation of the disturbance-relevant swimming performance.

Unfortunately, only very few studies have examined swimming speeds maintained for about 3-5 min until fatigue (Wolter & Arlinghaus 2003). Using a precautionary approach, no hydrodynamic impacts are to be expected if the physical forces meet the critical swimming performance of fish. Therefore the critical swimming performance was calculated for fish up to 200 mm total length (Figure 3), as small fish normally have the lowest swimming ability, and hence are more prone to hydrodynamic impacts.

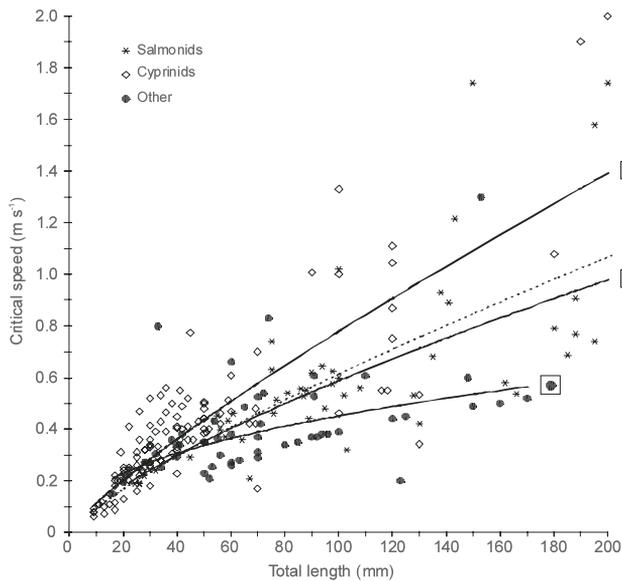


Fig. 3: Critical swimming performance of all fish pooled up to 200 mm total length (TL) (dotted line, $U_{crit} = 0.0158 * TL^{0.80}$, d.f. = 239; $R^2 = 0.65$; $p < 0.001$), salmonids ($U_{crit} = 0.0198 * TL^{0.74}$; d.f. = 49; $R^2 = 0.71$; $p < 0.001$), cyprinids ($U_{crit} = 0.0165 * TL^{0.84}$; d.f. = 111; $R^2 = 0.76$; $p < 0.001$) and other species ($U_{crit} = 0.0654 * TL^{0.42}$; d.f. = 50; $R^2 = 0.33$; $p < 0.001$).

The critical swimming performance differed significantly between taxonomic orders. Surprisingly, the critical performance of rheophilic cyprinids significantly exceeded those of salmonids as generalist swimmers (Webb 1984). According to our model, a critical swimming speed of 1 m s^{-1} will be performed by a 179 mm long fish, however, in this mode a 133 mm long cyprinid swims as fast as a 201 mm long salmonid (Figure 3).

Hydrodynamic features of waterways

Inland waterways are regulated rivers and canals serving as navigation routes. River engineering work for navigation purposes resulted in straightening, narrowing and deepening of main channels, and the loss of floodplains, abandoned waters and shallow shore line habitats. The corresponding dramatic losses of fish diversity have been widely documented (e.g. Nielsen et al. 1986, Brookes & Hanbury 1990, Adams 1993, Zauner & Schiemer 1994, Murphy et al. 1995, Wolter & Vilcinskas 1997, 2000, Arlinghaus et al. 2002). Beside the extension-related indirect impacts of navigation on habitat diversity, there are ongoing operation-related direct impacts of shipping on the aquatic biocoenoses. Each single vessel navigating through a waterway generates hydraulic disturbances in the form of waves and currents, mainly dynamic water level sinkage (drawdown), return currents opposite to the direction of movement, slope supply currents, wash waves, and propeller jet (Figure 4). Direct impacts on fish caused by the above mentioned navigation-induced physical forces have been commonly proposed (Holland & Sylvester 1983, Holland 1986, 1987, Nielsen et al. 1986, Zauner & Schiemer 1994, Wolter & Vilcinskas 1997, Adams et al. 1999, Killgore et al. 2001, Arlinghaus et al. 2002, Gutreuter et al. 2003).

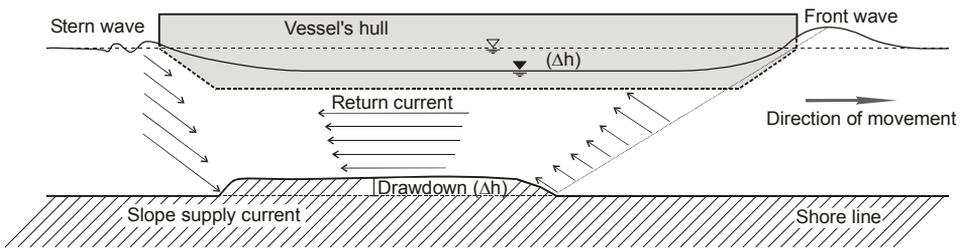


Fig. 4: Main physical effects induced by navigation in restricted waterways (thin lines illustrate the flow patterns).

Typically, totally decoupled from biology and ecology, in inland waterways civil engineers determine the physical forces during vessel passages to ensure navigation (e.g. Kuo et al. 1989, Oebius 2000 a), increase 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 & Adams 1989, Kuo et al. 1989, Fuehrer 1998,

Oebius 2000 b), determine critical tow speeds (e.g. Bhowmik et al. 1995, Hüsigg et al. 2000), decrease resuspension of fine sediments (e.g. ten Brinke et al. 1999), and to improve the economic performance of navigation by faster vessels (e.g. Hüsigg et al. 2000).

Hydrological studies of navigation effects on embankment structures revealed 0.05-0.45 m drawdown, 0.7-1.1 m s⁻¹ bank-directed current velocities, and up to 0.7 m wash waves (Fuehrer 1998, Hüsigg et al. 2000, Heibaum & Soyeaux 2002) during the passage of a commercial vessel. Thus, German waterway standards require designing embankments to withstand drawdowns of 0.6 m and bank-directed currents of 2 m s⁻¹ (Fuehrer 1998). The main hydraulic impacts generated by a passing vessel last typically for about 60 s, in maximum up to 2-3 min, depending on vessel speed and length (Bhowmik et al. 1995, Fuehrer 1998, Oebius 2000a, Arlinghaus et al. 2002, Heibaum & Soyeaux 2002). The frequency of hydraulic impacts due to passing vessels strongly depends on the economic importance of a certain waterway, and ranges between an daily average of 107 commercial vessels at lock Iffezheim, Rhine River, in 2003 to 1.2 at lock Havelberg, Havel River, in 2001 (German inland navigation statistics at www.elwis.de/Verkehrsstatistik).

In summary, a typical moving commercial towboat creates hydrodynamic forces of 0.7 m s⁻¹ for about 1 min occurring along the whole bank line of the navigation route, repeatedly daily. Intuitively, one might assume that these pulsed dynamic flow fields acting along the banks (and hence the nurseries of most freshwater fish) must play a structuring role for fish communities in waterways. However, *in situ* measurements of this effect are largely missing. Evidence can be derived from the swimming performance models introduced in this paper.

Ecological constraints to fish

Commercial navigation traffic generates maximum hydraulic forces close to the shore in the upper half of the bank slope (Mazumder et al. 1993, ASCE Task Committee 1998), where most fish have their essential, low flowing, littoral nursing areas (e.g. Scheidegger & Bain 1995, Staas & Neumann 1996, Lamouroux et al. 1999, Bischoff 2002). In contrast to other locally restricted hydrodynamic impacts, like hydropeaking, weirs or culverts, navigation-induced physical forces act at all shoreline habitats along the course, typically along the whole waterway, and thus, in the main channel, fish seem generally unable to avoid them. Because most of the freshwater fish juveniles depend essentially on the availability of shallow, low flowing shore line refuges for feeding and shelter, the discrepancy between navigation-induced currents and swimming performance becomes significant.

Freshwater fish hatch at total lengths of 2.7-9.5 mm and swim free between 6-15 mm. In this stage, their burst and critical swimming speeds range from 0.06-0.20 m s⁻¹ and 0.05-0.13 m s⁻¹ respectively (Figures 1, 2), which are significantly below the navigation-induced physical threshold of 0.7 m s⁻¹ at the shore line. The latter speed will be maintained by a 42 mm long fish in the burst mode and by a 71 mm in the critical mode. During the growth period to reach these minimum lengths, fish are limited to use of the

essential nursery areas, which led to the inference of the navigation-induced habitat bottleneck hypothesis by [Wolter & Arlinghaus \(2003\)](#). The bottleneck emerges when the navigation-induced currents exceed the maximum swimming performance of fish and washes them out, displaces them or otherwise prevents them from feeding, and it may become a structuring factor of fish assemblages if the offspring will be significantly depleted ([Arlinghaus et al. 2002](#); [Wolter & Arlinghaus 2003](#)).

This phenomenon was indicated by findings of [Arlinghaus \(2000\)](#) and [Arlinghaus et al. \(2002\)](#): In the canal Oder-Havel-Kanal (Germany), perch (*Percia fluviatilis*) a species with pelagic larvae, had far higher annual recruitment relative to roach (*Rutilus rutilus*) with shore-bounded larvae, although habitat and nutrient conditions would favor roach over perch. The reason for this observed fish community shift was suggested to be a comparatively higher mortality of shore-bounded roach larvae which were exposed to the most severe navigation impacts there.

However, the amount of fish kills and injuries depends not only on the strength and duration of single navigation-induced disturbances, but also on their frequency. In addition to all mechanical impacts of navigation on fish, direct or indirect (see [Wolter & Arlinghaus 2003](#) for a review and literature references), with an increasing disturbance frequency, even simple displacement or prevention from feeding become serious hazards for fish. Fasting for few days can cause significant reductions in white muscle glycogen stores, one of the three endogenous fuels for fast movements ([Kieffer & Tufts 1998](#)). Because burst exercise is largely supported by anaerobic glycolysis within the white muscle ([Kieffer 2000](#), [McFarlane & McDonald 2002](#)), decreased glycogen levels ultimately limit the anaerobic capacity of fish, and therefore, fasted fish display a lower burst performance compared to fed fish ([McFarlane & McDonald 2002](#)). Accordingly, even low amplitudes of hydrodynamic impacts may increase energy deficits of the fish.

Further studies are urgently needed to determine the critical frequency of disturbances which lead to a significant reduction of fish recruitment in waterways. Moreover, an evaluation of the NBH requires thorough *in situ* studies or experimental set-ups that closely resemble the hydrodynamic and ecological conditions of waterways, which is a considerable challenge. The models and hypotheses introduced here should be helpful in the establishment of a more precautionary management of inland waterways aiming to sustain fish diversity in highly modified water bodies, set against the background of the new Water Framework Directive of the European Union.

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