Critical swimming speed: its ecological relevance

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Abstract

Critical swimming speed ($U_{crit}$) is a standard measurement to assess swimming capabilities of fishes. To conduct this measurement a fish is introduced into a water tunnel in which the current velocity can be controlled by the investigator. At the beginning of the measurement water velocity is low, approximately 1 body length (BL) s$^{-1}$, and is then incrementally increased at prescribed intervals. Fishes tend to maintain their position in the water tunnel against the current until fatigue sets in. The time and velocity at which the fish fatigue are used to calculate the critical swimming speed. This procedure is widely used to assess the effects of environmental conditions and pollutants on fish performance. Since the procedure is conducted in conditions that are far from representing most natural environment experienced by fishes, doubts have been raised about its ecological and ecophysiological relevance. Few studies examined correlations between critical swimming speed and traits that seem to be more ecologically relevant. Positive correlations were found between $U_{crit}$ and routine activity, metabolic rates and body size of open water, planktivorous fishes, metabolic rates and body size. These data indirectly suggest ecological relevancy of $U_{crit}$, but direct measurements relating $U_{crit}$ to reproductive success or survival are required to assess such relevancy. © 2001 Elsevier Science Inc. All rights reserved.

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1. Introduction

Swimming performance is considered a main character determining survival in many species of fish and other aquatic animals (Jones et al., 1974; Taylor and McPhail, 1986; Graham et al., 1990; Rome et al., 1992; Young and Cech, 1993; Stobutzki and Bellwood, 1994; Swanson, 1998). Most fishes lack other weapons against predators, and thus swimming is their main way to avoid and survive their attack (Videler, 1993; Reidy et al., 1995; Watkins, 1996). Moreover, it is assumed that the maximal swimming performance may strongly influence the ability of a fish to obtain food, find a mate, avoid unfavorable conditions, and so on (Drucker, 1996). Thus, although rarely proven, it is suggested that swimming capability is a major trait effecting Darwinian fitness (Reidy et al., 2000). To evaluate the effects of different environmental conditions or pollutants on fish fitness or survival in an ecological system, a reliable, ecologically relevant measurement of swimming capability is required.
Fishes swimming performance are classified into three categories: sustained, prolonged and burst (Beamish, 1978). Sustained swimming speed defines those speeds that can be maintained by a fish for long periods [> 240 min (Beamish, 1966) or > 200 min (Brett, 1967)], and that are fueled aerobically. Prolonged swimming speed is also fueled aerobically, but is of shorter duration [20 s–200 min (Beamish, 1978)] than sustained, and ends in fatigue of the fish. Burst swimming speed is the highest speed of which fishes are capable, and can be maintained only for short periods [< 20 s (Beamish, 1978)], and is considered to be fueled anaerobically.

Sustained swimming speed is performed without resulting in muscular fatigue. Naturally, it includes cruising speed (e.g. migrating fishes), the velocity which negatively buoyant species must achieve to maintain hydrostatic equilibrium, and speeds for routine activity like spontaneous swimming, foraging and station holding (Reidy et al., 2000).

Fishes usually use burst swimming speed when trying to catch prey or to avoid a predator attack, as well as in any other situation of sudden disturbance and maneuvering through strong current fields (Reidy et al., 2000).

Prolonged swimming speed is very difficult to separate from sustained swimming speed in the natural habitat, because rarely, if ever, can fatigue be assessed in the field. On the other hand, prolonged swimming speeds are most accurately measured in the laboratory in a swimming tunnel (Beamish, 1978), because fatigue is easy to determine. However, some studies concluded that it is a behavioral, not only physiological phenomenon (Nelson, 1990).

2. Critical view on critical swimming speed methodology

There are several methods of measuring the aerobic swimming capability of fishes. The main three methods are (a) critical swimming speed (Brett, 1964); (b) endurance (Beamish, 1978); and (c) gait transition speed (Drucker, 1996).

An endurance test measures the time a fish can swim continually against a prescribed constant water velocity. During this measurement many fish should be examined individually at different speeds, and thus, this measurement is highly time consuming, and not favorable.

Gait transition speed measurement was recently suggested by Drucker (1996). In this method a fish is placed in a water tunnel and swims against incrementally increased speed. Some fish species use median and paired fins (MPF) swimming propulsion at slow swimming speed and shift to body and caudal fin (BCF) swimming propulsion at higher swimming speeds (Webb, 1993a). By observing the fish in the water tunnel, the investigator can determine the swimming speed at which the fish shifts from one gait to another. This method is rather new in fish swimming studies and no data are available yet to evaluate it. Anyway, this method is applicable only for those species that conduct such gait transition in swimming. Many fishes, especially pelagic species, use only one swimming mode for all swimming speeds, and cannot, therefore, be measured using this method.

Ever since Brett’s work (Brett, 1964), the most common way to measure swimming performance of fishes (or other aquatic organisms, e.g. tadpoles, squid, etc.) has been by the procedure of critical swimming speed (for review see Beamish, 1978; Hammer, 1995; Kolok, 1999). Brett (1964) was the first to develop and use this method. For the measurement, a fish is placed in a water tunnel or flume and forced to swim against water current at different velocities. Fishes usually tend to hold their position against the current due to ‘opto-motor’ response. In some studies an electrified downstream screen was used to force the fish to swim against the current (Beamish, 1978). According to the commonly used experimental protocol, prior to the measurement the fish is introduced into the water tunnel and left in the water at water velocity of 0.5–1 body length (BL) s⁻¹ to recover from handling stress before experiments begin. The recommended recovery duration is 8–12 h because metabolic rate measurements show that this is the period required for the fish to recover from handling stress. However, recent studies showed no significant difference in Uₘₓ between fish left to recover overnight and fish left to recover 1–2 h (Kolok, 1991; Peake et al., 1997). After the recovery period, the water velocity is increased at a prescribed increment (usually 0.5–1 BL s⁻¹) for a prescribed duration (usually 10–60 min) and at the end of this duration water velocity is increased again in the prescribed increment
for the next interval (Farlinger and Beamish, 1977; Kolok, 1999). After several intervals and increments the fish is fatigued and is swept downstream to a net screen located at the downstream end of the water tunnel that prevents the fish from being carried out of the working section of the water tunnel. At this stage the measurement ends and critical swimming speed \( U_{cri} \) can be calculated (Brett, 1964, 1967):

\[
\frac{U_{cri}}{U_i} = 1 + \left[ U_i \left( T_f / T_i \right) \right]
\]

where \( U_i \) is the highest velocity maintained for the whole interval (cm s\(^{-1}\)), \( U_f \) is the velocity increment (cm s\(^{-1}\)), \( T_i \) is the time elapsed at fatigue velocity (min), and \( T_f \) is the prescribed interval time (min). Critical swimming speed can be presented as absolute swimming speed (cm s\(^{-1}\)) or as relative swimming speed [BL s\(^{-1}\)]. As this measurement is based on fish fatigue, it uses, by definition, prolonged swimming speeds to evaluate swimming performance.

Critical swimming speed is frequently used to evaluate the effects of different factors on fish swimming ability, usually in order to predict their ecological effects on fishes in their habitat. These factors include environmental conditions such as temperature (Jones et al., 1974; Keen and Farrell, 1994; Taylor et al., 1996; Adams and Parsons, 1998; Kieffer et al., 1998), salinity (Nelson et al., 1996; Kolok and Sharkey, 1997; Swanson et al., 1998; Plaut, 2000a), feeding rate (Gregory and Wood, 1998), body form (Nicoletto, 1991; Plaut, 2000b), effects of externally attached tags (Davidson et al., 1999) and transmitters (Counihan and Frost, 1999), and toxicological effects of pollutants (Beaumont et al., 1995a,b; Hammer, 1995; Heath, 1995; Kennedy et al., 1995). A discussion of the problem of comparing different data sets due to different methodologies (mostly prescribed increments and intervals) has recently been published (Kolok, 1999).

Critical swimming speed is the easiest available method of measuring swimming performance. However, since it is in the range of prolonged swimming speeds that rarely, if ever, occur in nature, one may wonder if this measurement is ecologically relevant, and if it can predict Darwinian fitness and survival.

Moreover, in Brett-type (Brett, 1964) or Blazka (Blazka et al., 1960) water tunnels (or their modifications), which are usually used to measure critical swimming speeds, the flow/swimming conditions are far from resembling any existing natural habitat experienced by most fishes (excluding, maybe, fishes swimming upstream in high velocity rivers and against fast tidal currents). There are several potential sources of artifacts in the commonly used water tunnels.

1. Flow characteristics: the water flow in water tunnels is usually straightened with a block of plastic straws or other kinds of small diameter pipes, with the aim of producing laminar water flow (Bell and Terhune, 1970). However, fully laminar water flow is rarely achieved, if ever. In most cases the water flow is 'uniformly microturbulent' (Gordon et al., 1989; Plaut and Gordon, 1994). Fishes in their natural habitat, in which they swim mostly in calm or turbulent water, may rarely experience this kind of flow.

2. Wall effect: in a water tunnel, a boundary layer is created near the walls, ceiling, and floor. The width of this boundary layer is usually negatively related to water velocity in the water tunnel. Thus, a fish may find places with slower velocities (than the prescribed velocity) near the walls, floor and ceiling during the experiment. The ability to do this is water velocity dependent. In addition to the boundary layer, a fish may experience pressure resonance of its own movement and wake from the walls. Thus, a fish may swim at different speeds than those prescribed. Webb (1993a) studied wall effects in the steelhead trout, Oncorhynchus mykiss, and found that FH, the product of tail beat frequency and tail beat amplitude, decreased as spacing between solid walls, and concluded that a fish work less hard when swimming near a solid wall. However, \( U_{ci} \) was lower for fish swimming in narrow space between solid or grided walls compare to controls.

3. Blocking effect: the fish itself, by blocking part of the cross-section area of the tunnel, creates a faster velocity (than the prescribed velocity) and a different pressure regime in the vicinity of its own body. This effect is commonly corrected by calculation when the fish maximum cross-section area is > 10% of the water tunnel cross-section (Bell and Terhune, 1970).
In summary, the environment that a fish experiences in a water tunnel under the common experimental protocol of measuring critical swimming speed is rarely, if ever, experienced by fishes in their natural habitat. Therefore, it is not trivial that measurement of critical swimming speed should be ecologically relevant and capable of predicting Darwinian fitness and survival chance.

The ideal way to establish such relevancy would be to mark fish with known pre-measured swimming abilities (measured as critical swimming speed of each individual), release them into their natural habitat, and follow their reproductive success, or more practically, to recapture them, and then correlate their survival with their individually pre-measured critical swimming speeds. To my knowledge such an experiment has never been published.

The objective of this paper is to examine the ecological relevancy of critical swimming speeds. Since no direct data exist yet to establish such a relevancy, correlations between critical swimming speeds and other recent measurements that are more likely to be ecologically relevant are examined.

3. Correlations and clues for ecological relevancy of critical swimming speed

One of the essential conditions for Darwinian natural selection is an inter-individual variation of the trait within population (Darwin, 1859). Critical swimming speed data, as well as other locomotion performances, are known to be highly variable (Berry and Pimentel, 1985; Watenpaugh and Beitinger, 1985) and were considered to reflect a statistical ‘noise’. However, several recent studies clearly demonstrated that inter-individual variation is a repeatable phenomenon and reflects a real inter-individual variability in the swimming capacity of fishes. Such repeatable variation in critical swimming speed was found for several fish species, e.g. largemouth bass (Micropterus salmoides) (Kolok, 1992), northern squawfish (Psychocheilus oregonensis) (Kolok and Farrell, 1994), rainbow trout (Oncorhynchus mykiss) (Gregory and Wood, 1998), and Atlantic cod (Gadus morhua) (Nelson et al., 1994; Reidy et al., 2000). In addition, Plaut and Gordon (1994) showed that variability of active metabolic rate in the zebrafish (Danio rerio) was significantly lower for gynogenetic isogenic homozygous diploid clonal strain than in wild-type strain. These repeatable inter-individual variations and genetically related variation suggest that individual critical swimming speed may represent a characteristic that significantly affects Darwinian fitness.

There are numerous studies on the effects of environmental conditions on critical swimming speeds (for review see Beamish, 1978; Randall and Brauner, 1991; Hammer, 1995; Kolok, 1999). However, in most of them the critical swimming speed is the only dependent variable, and the ecological, or Darwinian fitness relevancy, is only suggested, if mentioned at all. Thus, there is no direct proof for such relevancy.

A trait that seems to be ecologically relevant is routine, or spontaneous activity level, especially for naturally active planktivorous fishes. The primary function of routine swimming is foraging (Blaxter and Staines, 1971; O’Brien, 1979; Fuiman and Webb, 1986), as well as migration and predator avoidance (Blaxter and Staines, 1971; Hunter, 1972; Blaxter, 1986; Zhou and Weis, 1999), all of which strongly affect Darwinian fitness and survival chance. This relation was directly demonstrated by Walton (1988) who showed that variation in frequency of movement was related to variation in the amount of prey consumed by the Fowler’s toad (Bufo woodhousii fowleri) under natural conditions. Some examples of correlation between routine activity level and standard metabolic rate with critical swimming speed follow.

Plaut (2000a) measured critical swimming speed, routine activity and standard metabolic rate in the killifish (Aphanius dispar) acclimated to a wide range of salinity [freshwater to 400% seawater (140 ppt)]. At high salinities (> 200% seawater), both critical swimming speed and routine activity level were reduced, and both traits were significantly correlated (Fig. 1). The two traits were also correlated with standard metabolic rate. It was suggested that these reductions in critical swimming speed and routine activity level are a result of decreased permeability of the gills and skin, a reaction to high osmotic pressure, which also decrease oxygen uptake. These reductions may also be a result of a third trait, such as increased cortisol concentration, etc., which is affected by stressful conditions, and in turn, affects swimming and activity.

A. dispar frequently inhabits water of high
salinity, and this fact raises the question of how this species survives in spite of the fact that the salty conditions decrease its ability to gain food and avoid predators. Plaut (2000a) suggests that since such a habitat is undesirable for other fish species, predators and/or competitors, A. dispar can exploit such an environment without competition or predation risk even though its swimming ability and routine activity level are reduced.

Similar results were found by Swanson (1998) for milkfish (Chanos chanos) in different salinities. In this study, some of the fish did not reach fatigue at the maximum velocity of the water tunnel, so the value $U_{\text{crit}}$ represents only the slower fish, and the value $U_{\text{max}}$ represents both $U_{\text{crit}}$ of the slower fish and the highest velocity of the water tunnel for fish that did not reach fatigue. Thus, $U_{\text{max}}$ is an underestimation of actual critical swimming speed. Swanson (1998) measured routine swimming speed ($U_{\text{routine}}$) as well, which may adequately represent spontaneous activity. When this trait was tested in salinities of 15, 35 and 55 ppt, maximum swimming speed (underestimation of critical swimming speed) was significantly higher at 15 ppt than at 55 ppt (and at 35 ppt in between). Routine swimming speed was higher at 35 ppt than at 15 ppt, and at 15 ppt it was higher than at 55 ppt. Thus, in milkfish, routine swimming speed was correlated with critical swimming speed only at the two extreme salinities. However, since the actual critical swimming speed is yet unknown, and since inter-individual variation was high, these results should be treated carefully.

Critical swimming speed and routine activity level were also tested for zebrafish (Danio rerio) in relation to caudal fin size (Plaut, 2000b). In this case the differences between treatments were morphological rather than environmental. Zebrafish of three types were tested: (1) the wild type, characterized by short, stiff caudal fin; (2) the long-finned type, characterized by an extended, softer caudal fin, being approximately twice the length of the wild type caudal fin (Tan and Phang, 1994); and (3) the no-tail type that, due to a well known mutation, lack caudal fin completely (Schulte-Merker et al., 1994). Critical swimming speed of wild type was the highest (56.0 ± 4.8 cm s$^{-1}$), while that of long-finned was significantly lower (43.7 ± 6.8 cm s$^{-1}$), approximately 78% of wild type critical swimming speed. Critical swimming speed of no-tail was the lowest (19.8 ± 4.7 cm s$^{-1}$), approximately 35% of that of wild type. Routine activity level of wild type was also significantly higher than long-finned, which in turn was significantly higher than the routine activity level of no-tail. Thus, there is a close correlation between the two measurements (Fig. 2).

Zebrafish are open water, active planktivorous fish. As in A. dispar, it is expected that zebrafish which are less active will be at a disadvantage for overcoming natural selection pressures when competing with wild type individuals in their natural habitat. Since captive populations of ze-
brafish originated from many individuals captured in rivers in south-east Asia over many years (Laale, 1977), and since long-finned and no-tail mutations occur quite often in captive populations, it is probable that these mutations also occur in natural populations as well. As these mutations are, however, not known in natural populations, although long-fin is a genetically dominant trait, it is reasonable to suppose that in nature these mutants do not survive.

Other factors associated with Darwinian fitness and positively correlated to critical swimming speed were listed by Kolok (1999), including coloration, male territoriality, etc. Kolok (1999) considered growth rate a factor associated with Darwinian fitness as well, and provided data showing that growth rate is negatively correlated with critical swimming speed (Kolok and Oris, 1995; Gregory and Wood, 1998, 1999). This may be related to the fact that well-fed fish have slower critical swimming speed, probably due to energy allocation to specific dynamic action (SDA) (Alsop and Wood, 1997). However, it is well documented that body size is positively correlated with critical swimming speed (Beamish, 1978), and large body size in fishes is often considered a Darwinian fitness factor because larger fish have been shown to be socially dominant (Abbott et al., 1985) and to have preferential access to food (Fausch, 1983; Metcalfe, 1986, reviewed in Kolok, 1999).

Another study that demonstrates the correlation between swimming capability and predation risk was done on tadpoles. Watkins (1996) measured burst swimming speed of the Pacific tree frog (Pseudacris regilla) and showed that slower tadpoles were more vulnerable and preyed more upon by water snakes than were faster tadpoles. Although the swimming capacities were not measured by the critical swimming speed method, the results clearly demonstrate the significance of locomotion capability in surviving natural selection forces. Similar results were presented for coho salmon (Oncorhynchus kisutch) (Taylor and McPhail, 1985).

In many fishes, burst swimming speed, the fastest, anaerobic speed, is more useful to avoid predator attack and to gain food than sustained swimming speed. Reidy et al. (2000) studied aerobic (sustained) and anaerobic burst (swimming against rapidly increased water current) and sprint (fast start) swimming capability of the Atlantic cod, and found that individuals that perform well in the $U_{crit}$ test also perform well in the sprint test, but $U_{crit}$ and burst performance was negatively correlated. Aerobic and anaerobic activities differ in their mechanisms, thus, it may be expected that a trade-off exists between them. On the other hand, one may expect individuals to be either 'good athletes' or 'bad athletes' (Bouchard et al., 1988, 1989). The study by Reidy et al. (2000) was the first work that examined the relation between $U_{crit}$ and anaerobic capacity in fishes and it suggested that a such positive correlation may exist. If this is the situation, $U_{crit}$ data may represent anaerobic capability as well. However, more comparative data are required in order to establish such correlations.

The above examples demonstrate close correlations between critical swimming speed (or other locomotion capabilities) and other, ecological relevant traits.

4. Discussion

Many authors have used and suggested critical swimming speed as an ecologically relevant measurement. Jain et al. (1998) stated that in terms of ecological relevance, critical swimming speed is a good indicator of the ability of a salmon to swim through stretches of strong current during its upstream migration. The critical swimming speed measurements give at least a rough estimate of the maximal aerobic swimming velocity in fishes (Brauner et al., 1994), and are generally assumed to reflect maximum oxygen consumption capability (Farrell and Steffensen, 1987). Moreover, Brauner et al. (1994) suggested that, although the interpretation of critical swimming speed results is limited because it cannot possibly take into account variables crucial for survival, such as behavior, these results provide a relative index by which the physical status of the fish can be quantified and compared.

Hammer (1995) stated that critical swimming speed values yield information comparable with LD$_{50}$ values in toxicological studies. However, it seems that critical swimming speed measurements are much better and more useful in toxicological research. LD$_{50}$ tests examine the concentration related effects of acute exposure to toxicants. In most cases, animals are exposed to
chronic exposure by pollutants. Critical swimming speed tests can measure sub-lethal effects of chronic exposure and provide more accurate and relevant information about the ecosystem in the polluted habitat. Indeed, most studies showed decrease of critical swimming speed as pollutant concentrations increased (for review, see Hammer, 1995).

It is agreed that reduction in critical swimming speed is usually a result of interference of oxygen uptake in the gills or reduction of blood oxygen transport (due to Bohr and Root effects, Hammer, 1995), and thus, reduction in critical swimming speed demonstrates reduction in general aerobic capacity.

By contrast, Webster and Webster (1988) argued that the assumption that high rates of physiological processes are actually important components of fitness may well be correct, but although plausible, it is a speculation, not a hypothesis. Pough (1989) stated that, in most cases, the assumption that measurements of performance made in the laboratory are relevant for animals under natural conditions is based more on hope than on any objective evidence.

However, as detailed above, several recent studies on intra- and interindividual variation in locomotion performance of fishes (Kolok, 1992; Gregory and Wood, 1998; Kolok et al., 1998), and on the affect of locomotion capacity on survival (Taylor and McPhail, 1986; Jayne and Bennett, 1990a,b; Watkins, 1996), suggest that this assumption is, at least, not entirely incorrect.

In conclusion, it is agreed that data on critical swimming speed are individually repeatable, reflect maximum aerobic capacity, and yield comparable data on the general swimming ability of the fish. It has not yet been positively proven that critical swimming speed can be directly correlated to Darwinian fitness and survival, but it is reasonable to assume that this measure is at least a rough estimate of the ability of a fish to conduct activities in which swimming is involved. Since this is the most convenient way devised yet to measure swimming performance without harming the fish, critical swimming speed is probably the best ecophysiological measurement to estimate swimming performance capability and to predict ecological consequences, especially for riverine fishes that migrate upstream or fishes that hold their position against currents, and pelagic planktivorous fishes.

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