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# The Effects of Environmental Factors on the Physiology of Aerobic Exercise

D.J. McKenzie<sup>1</sup> and G. Claireaux<sup>2</sup>

## INTRODUCTION

Fishes can be found in almost any body of water, be it an underground cave, beneath the arctic ice, in the deepest marine trench, in a fast moving mountain stream, or on a tropical reef. In each of these environments, fish have evolved combinations of physiological, morphological and biomechanical traits which adapt them to their particular habitat. In particular, almost all fish swim. Many functional traits are integrated to perform swimming activities, at many different levels of organisation ranging from cell energy production, to myocyte and muscle contraction, to cardiac and respiratory function, and to the systems for neural and endocrine regulation, integration and control. These traits have presumably all co-evolved, and contribute not only to locomotion but also to environmental adaptation in its broadest sense. It is generally held that the diversity of fish swimming modes and performance is a direct reflection of their ecological diversity. For instance, illuminated open

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oceans may select for high locomotory capacity, with a streamlined drag-minimising, torpedo-shaped morphology. In the abyss, on the other hand, the absence of light and the reduction in the distance over which predators and prey interact may have relaxed selection pressures on the body shapes and swimming abilities of the resident fish (Verity *et al.*, 2002; Seibel and Drazen, 2007). It seems intuitive that swimming ability should contribute directly to ecological performance and evolutionary fitness in fishes, although there is currently very little direct experimental evidence for this (Billerbeck *et al.*, 2001; Lankford *et al.*, 2001; Ghalambor *et al.*, 2003). Nonetheless, the assumption that swimming performance is of ecological significance has been the impetus for many studies to understand the anatomical and physiological mechanisms that contribute to swimming performance, and how performance is influenced by factors in the environment (Domenici *et al.*, 2007).

There are a number of reasons why environmental factors can be expected to influence swimming performance in fishes. The vast majority of fishes are poikilotherms whose biochemical and physiological rates are controlled by water temperature (the exceptions being some large oceanic species such as the tunas and lamnid sharks, see Bernal *et al.*, 2001; Block *et al.*, 2001; Graham and Dickson, 2004, for reviews). Water is not ideal as a respiratory medium, because of its high specific density and low capacitance for dissolved oxygen. This means that fishes ventilate high volumes of water across a very large surface area of delicate respiratory epithelium. As a result, variations in factors such as water salinity, dissolved carbon dioxide, and also pollution, can challenge physiological homeostasis. Finally, fishes interact chemically with their environment through their diet, with profound effects on their body composition and physiology. By investigating how all such environmental factors influence fish swimming performance, we should improve our understanding of their life history strategies and our ability to predict the impact of environmental change.

### **Muscle Types and Categories of Exercise**

All fish groups possess two prominent myotomal muscle masses on either side of their body which are used for swimming with undulations of the body and caudal fin (Bone, 1978; Shadwick and Gemballa, 2006; McKenzie *et al.*, 2007a). Extensive reviews of the structure, innervation and function of these muscles in fishes are provided by Bone (1978), S  nger and Stoiber (2001), Shadwick and Gemballa (2006) and Syme (2006). Of significance in the context of the current review is the distinct anatomical and metabolic division of the muscle fibres. ‘‘Slow oxidative’’ fibres have, as the name implies, a slow twitch frequency that relies almost exclusively upon oxidative phosphorylation to provide ATP. They are well-vascularised to provide the O<sub>2</sub> and exogenous nutrients for oxidative work, and contain myoglobin, hence

the common name “red muscle”. Red muscle typically represents a minor proportion of the muscle mass and is used for steady aerobic swimming at relatively slow speeds. “Fast glycolytic” fibres have a fast twitch frequency and rely almost exclusively upon endogenous anaerobic fuels, initially phosphagen hydrolysis and then anaerobic glycolysis. These “white muscle” fibres are less well vascularised and lack myoglobin, they comprise the main part of the myotome and are used for short bursts of high-speed swimming (Bone, 1978; Webb, 1998; Sanger and Stoiber, 2001). Some fish species also possess intermediate fibres, “pink muscle”, which is intermediate in terms of its distribution, energy metabolism, and role in steady versus burst swimming. Bone (1978) has argued that the large muscle mass reflects the density of the medium in which fish live, which exerts great friction drag, while the anatomically discrete muscle types reflect the conflicting demands of allowing both low speed cruising economy and also short bursts of high speed. Fish can also swim by movements of median and paired fins (Webb, 1998; Korsmeyer *et al.*, 2001; McKenzie *et al.*, 2007a). These swimming modes have been much less well studied than body/caudal fin swimming. In teleosts these types of locomotion appear to be predominantly aerobic (Webb, 1998; Korsmeyer *et al.*, 2001), and the muscles tend to be slow twitch and oxidative (Webb, 1998).

Rhythmic body/caudal fin swimming activities have been categorised according to the muscle types and energetic substrates that they rely upon, and to their duration (Beamish, 1978; Webb, 1993, 1998). Two extremes are recognised. Sustained aerobic swimming is dependent upon red muscle function, with nutrients (primarily lipids) and O<sub>2</sub> supplied in the bloodstream (Jones and Randall, 1978; Richards *et al.*, 2002). Thus, performance of red muscle also depends upon cardiac muscle function and pumping capacity of the heart (Jones and Randall, 1978; Claireaux *et al.*, 2005). This type of swimming comprises relatively low tailbeat frequencies and speeds during, for example, foraging, maintaining position against currents, and migrating against little or no opposing water currents. It can, in theory, be maintained indefinitely without any eventual muscular fatigue (Webb, 1998). The other extreme is burst swimming, which is an anaerobic activity dependent upon white muscle function that can only be sustained for short periods (seconds) (Webb, 1998). This comprises the much higher tailbeat frequencies and swimming speeds that are achieved by recruiting the large white muscle mass, for example during predator-prey chases or when negotiating velocity barriers during upriver migration. The duration of burst swimming is presumably limited, ultimately, by the availability of endogenous white muscle stores of high energy phosphagens and glycogen (Wood, 1991; Richards *et al.*, 2002). Intermediate between these extremes are those speeds at which fish can swim for prolonged periods, but not indefinitely. Prolonged swimming presumably can involve

the recruitment of all muscle fibre types and therefore is a mixed aerobic and anaerobic activity. Such prolonged swimming speeds would be used for particular periods of up-river migration (Standen *et al.*, 2004) or perhaps elements of pursuit for predator prey interactions. The duration of prolonged swimming may be limited by cardiorespiratory capacity for O<sub>2</sub> and nutrient supply to the oxidative muscle and myocardium (Jones and Randall, 1978; Farrell, 2002, 2007) and/or when white muscle recruitment is too frequent and/or intense (Peake and Farrell, 2004). This chapter focuses upon the effects of environmental factors upon aerobic exercise, hence how these factors influence the ability of fish to perform sustained and prolonged swimming. The effects of environmental factors on anaerobic swimming performance are reviewed in Chapter 9, by Wilson *et al.* in this book.

### **Measuring the Performance of Aerobic Exercise: an Evaluation of the $U_{crit}$ Protocol**

The physiology and performance of aerobic swimming has been studied quite extensively in laboratory studies, using flumes and swimming respirometers, with the vast majority of work confined to salmonids (see reviews by Beamish, 1978; Jones and Randall, 1978; Webb, 1993, 1998; Videler, 1993). Various exercise protocols using flumes have been developed to measure traits such as maximum sustained swimming speed (see below) and maximum prolonged speed in fishes (Videler, 1993; Wilson and Egginton, 1994; Claireaux *et al.*, 2006), but the vast majority of studies have utilised the “critical speed” ( $U_{crit}$ ) protocol described by Brett (1964). Brett (1964) developed the protocol to mimic upriver migration by anadromous salmonids, presuming that these would be swimming against currents of ever higher velocity as they approached their spawning grounds in headwaters. Thus, the protocol submits a fish to incremental stepwise increases in swimming speed in a swim flume until it fatigues, and  $U_{crit}$  is then interpolated as a single performance trait (Brett, 1964; Randall and Brauner, 1991; Farrell, 2007; Fig. 10.1A).

During the initial stages of the protocol the fish utilises red muscle, provided with O<sub>2</sub> and nutrients by the heart. This allows elements of aerobic metabolic performance and energetics to be measured. The red muscle generates constant rhythmic tailbeats, which show a linear increase in frequency with swimming speed. This aerobic muscular work is associated with an exponential increase in O<sub>2</sub> demand as swimming speed increases (Brett, 1964; Beamish, 1978; Webb, 1993). Measurement of rates of O<sub>2</sub> uptake ( $M_{O_2}$ ) reveal that the maximum aerobic metabolic rate during the  $U_{crit}$  protocol is typically at least three-fold higher than basal (standard) metabolism (reviewed by Jones and Randall, 1978 and Randall, 1982 for

salmonids, see also Webber *et al.*, 1998; McKenzie *et al.*, 2001a, 2003a; Chatelier *et al.*, 2005, 2006 for examples of other species), with the highest maximum aerobic metabolic rate probably being in the tunas (see Korsmeyer and Dewar, 2001, for a review of the comparative respiratory metabolism and energetics of the tunas). This increased O<sub>2</sub> demand is met by an approximate doubling of water flow over the gills (whether by active or ram ventilation), and an up to five-fold increase in cardiac output in most teleosts (Jones and Randall, 1978; Thoraresen *et al.*, 1996; Gallagher *et al.*, 2001; Chatelier *et al.*, 2005, 2006; Claireaux *et al.*, 2005), with, once again, the tunas probably having the highest cardiac outputs of all teleosts during exercise (see Brill and Bushnell, 2001, for a review). The rise in cardiac output causes lamellar recruitment and so augments effective exchange surface at the gills, and blood O<sub>2</sub> carrying capacity may also be increased by release of erythrocytes from the spleen (Jones and Randall, 1978; Randall, 1982). There is, however, also a large increase in rates of O<sub>2</sub> extraction by the working muscle and, despite the concomitant rise in cardiac output, there is a profound decline in the O<sub>2</sub> tension of venous blood returning to the heart, and therefore a much larger arterio-venous O<sub>2</sub> partial pressure gradient across the gills (Stevens and Randall, 1967; Jones and Randall, 1978; Randall, 1982; Farrell and Clutterham, 2003).

At a certain speed, however, these aerobic adjustments are no longer sufficient and fish will be obliged to recruit the large white muscle mass in order to maintain position in the current (Wilson and Egginton, 1994). This is visible as a discrete change in swimming behaviour where short spurts of very high tailbeat frequencies are alternated with moments of passive coasting, such that the fish bursts forward and coasts back within the swim flume ("burst and coast" behaviour). This gait transition and recruitment of white muscle is typically associated with a plateau (asymptote) in both M<sub>O<sub>2</sub></sub> and rates of cardiac output, which can begin at speeds as early as 70% of the subsequent U<sub>crit</sub> (reviewed by Farrell, 2002, 2007; see also Wilson and Egginton, 1994; Lee *et al.*, 2003; Chatelier *et al.*, 2005). Thus, white muscle recruitment can contribute up to 30% to the top end of U<sub>crit</sub> performance, followed by fatigue, with the fish falling against the back screen of the flume. The actual U<sub>crit</sub> that is derived can depend upon the magnitude and duration of the increments in swimming speed, which should ideally be increments of between 0.5 and 1 bodylengths per second over at least 30 minutes (Beamish, 1978). The protocol is, therefore, an index of prolonged swimming performance that involves first red and then white muscle use (Beamish, 1978).

There is some debate about whether fish reach their maximum aerobic cardiorespiratory and exercise capacity during a U<sub>crit</sub> protocol, and about the factors which cause the transition from red to white muscle activity. By far the most information is available for salmonids of the genus *Oncorhynchus*,

in particular the rainbow trout, *O. mykiss*. Farrell (2007) argues that, prior to the transition to burst-and-coast swimming in salmonids performing a  $U_{crit}$  test, arterial blood is being pumped at the maximum rate by the heart, this arterial blood is fully saturated with  $O_2$ , and the venous blood has been depleted of  $O_2$  to the maximum possible extent. Thus, the rates of  $M_{O_2}$  measured at this point can be considered a good estimate of maximum aerobic metabolic rate and aerobic exercise capacity for these species (Farrell, 2007). There is excellent agreement between maximum *in-vivo* measures of cardiac output during a  $U_{crit}$  test and maximum *in vitro* measures of output in heart maximally stimulated with adrenaline in these salmonids (Claireaux *et al.*, 2005; Farrell, 2007). This matching of *in vivo* and *in vitro* cardiac pumping capacities has recently also been demonstrated for a non-salmonid, the European sea bass, *Dicentrarchus labrax* (Chatelier *et al.*, 2005, 2006; Farrell *et al.*, 2007). In rainbow trout, blood remains fully saturated with  $O_2$  throughout a  $U_{crit}$  protocol (reviewed by Jones and Randall, 1978; Farrell, 2007), and the capacity for  $O_2$  uptake at the gills and transport in the blood seems to be maximised at gait transition. Indeed, aquatic hyperoxia does not increase maximum aerobic metabolic rate or improve  $U_{crit}$  performance (Kiceniuk and Jones, 1977; reviewed by Jones and Randall, 1978; Farrell, 2007), and blood doping (polycythemia) only leads to minor improvements to these performance traits (Gallaughier *et al.*, 1995; reviewed by Farrell, 2007). Thus, the  $O_2$  demands of increased red muscle work during a  $U_{crit}$  protocol depend almost entirely upon the increase in cardiac output. This has led Farrell (2002, 2007) to propose that it is cardiac pumping capacity which defines maximum aerobic metabolic rate and aerobic swimming performance in salmonids. Perhaps the most direct evidence for this is that rainbow trout selected for high maximal cardiac output (*in vivo* and *in vitro*) can achieve higher maximum aerobic metabolic rate (and  $U_{crit}$ ) than animals with poorer maximal cardiac performance (Claireaux *et al.*, 2005).

McKenzie *et al.* (2004) measured partial pressures of  $O_2$  ( $PO_2$ ) in the red muscle of rainbow trout during  $U_{crit}$  swimming and found no evidence that  $O_2$  was depleted at the gait transition to white muscle use nor, indeed, at fatigue from  $U_{crit}$ . Thus, it would appear that it is not inadequate  $O_2$  supply to working red muscle which elicits the transition to anaerobic swimming. Farrell and Clutterham (2003) measured venous  $O_2$  tensions continuously during  $U_{crit}$  swimming and found that these never fell below a  $PO_2$  of about 3 kPa (20 mm Hg) and that the trout transitioned to burst-and-coast swimming when this lower asymptotic threshold was reached. The heart of trout derives its  $O_2$  supply in large part from venous return, and it will be the  $PO_2$  gradient from plasma to myocardium that will assure this supply (reviewed by Farrell, 2002, 2007). Thus, it has been proposed that the transition to white muscle occurs because myocardial  $O_2$  supply becomes

limited (Farrell and Clutterham, 2003; Farrell, 2007). These authors suggest that the transition is implemented to protect the heart from becoming hypoxic (Farrell and Clutterham, 2003; Farrell, 2007). This would imply that it is a behavioural response based upon information from, for example, a venous  $O_2$ -sensitive chemo-receptor (Barratt and Taylor, 1984). Presumably, fishes with greater cardiac pumping capacity would maintain a higher venous  $PO_2$  for any given degree of red muscle work, and hence the gait transition would be deferred to a higher speed. This remains to be demonstrated.

At fatigue from  $U_{crit}$  the red muscle of trout does not exhibit major metabolic imbalances (Richards *et al.*, 2002) or  $O_2$  depletion (McKenzie *et al.*, 2004). This raises the question of the selective advantage of having a system where maximum aerobic swimming performance is not limited by  $O_2$  delivery to red muscle but, rather, by venous  $O_2$  delivery to the heart. One possibility is that this allows the fish to repeat bouts of aerobic exercise with little intervening recovery. That is, as soon as the red muscle stops working,  $O_2$  delivery to the heart would be restored and a new bout of aerobic exercise can commence. Indeed many fish, not just salmonids, can repeat  $U_{crit}$  performance after only a very short period of intervening recovery (Jain *et al.*, 1998; McKenzie *et al.*, 2007b). It is not clear whether maximum aerobic swimming performance of other fish groups and species is also defined by cardiac pumping capacity, and venous  $O_2$  supply to the heart, not least because of a lack of information. There is some circumstantial evidence that cardiac performance limits maximum aerobic metabolic rate and  $U_{crit}$  in the European sea bass (Chatelier *et al.*, 2005, 2006; Claireaux *et al.*, 2006; Farrell *et al.*, 2007).

Given that the protocol was developed to mimic salmonid spawning migrations (Brett, 1964), the ecological significance of  $U_{crit}$  as a performance trait for other fish groups and species has been questioned (Plaut, 2001; Nelson *et al.*, 2002). Furthermore, because the experimenter effectively imposes the gait transition upon the fish, it has been suggested that fatigue is behavioural rather than due to physiological limitations such as substrate depletion in white muscle (McFarlane and McDonald, 2002; Peake and Farrell, 2006). That is, the fish may not be able to recruit white muscle effectively within the confined space of a swim flume, and so may prefer to fall back against the screen (Peake and Farrell, 2006). Thus, the  $U_{crit}$  protocol may be a profoundly artificial situation for a fish, not least because when swimming spontaneously against natural currents fish often swim with positive ground speed, especially following white muscle recruitment (Standen *et al.*, 2002, 2004; Peake and Farrell, 2004), whereas in the flume they must maintain position at zero ground speed as current velocity is increased.

Thus, aerobic swimming performance may be maximised during a  $U_{crit}$  protocol, but the actual trait itself is not a direct measure of maximum aerobic swimming performance because white muscle provides up to 30%



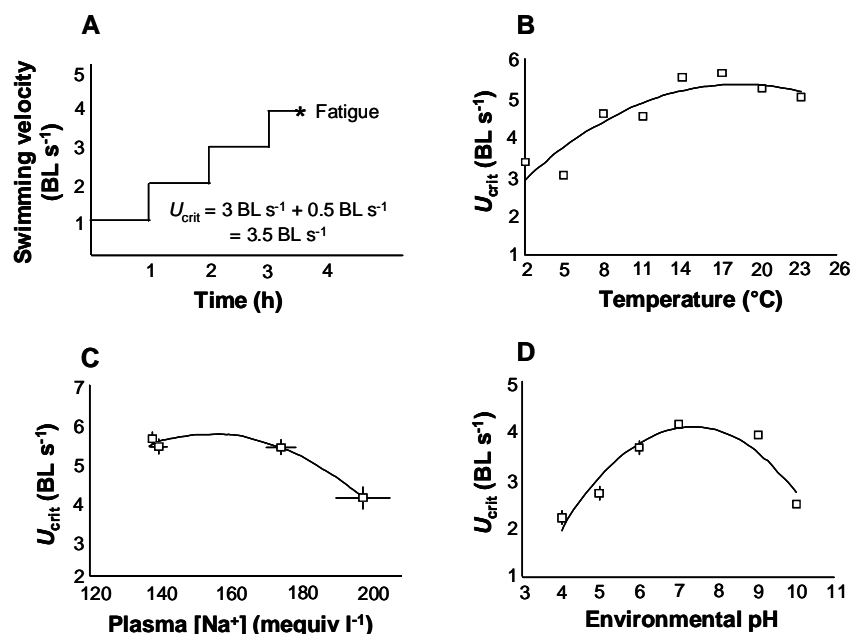
to the top end of the speed range. Then, it is not clear what actually causes fatigue, whether it is behavioural or physiological or both. Recent studies on wild migrating salmonids, and on fish spontaneously negotiating velocity barriers in long raceways, indicate that animals switch between red and white muscle recruitment as required, and may be able to achieve very much higher swimming speeds than those measured in a  $U_{crit}$  test without the subsequent metabolic imbalances that characterise anaerobic exercise (Standen *et al.*, 2002, 2004; Peake and Farrell, 2004, 2006; Castro-Santos, 2005).

Nonetheless, if the  $U_{crit}$  protocol is associated with measures of  $O_2$  uptake, it provides valid information about swimming metabolism and energetics, and therefore underlying aerobic performance. Individual  $U_{crit}$  performance is consistent and repeatable in a diversity of fish species, both in the short term (Jain *et al.*, 1998; McKenzie *et al.*, 2007b) and the long-term (Claireaux *et al.*, 2007), indicating that the protocol can be used to gauge and compare performance. Furthermore,  $U_{crit}$  performance is sensitive to a variety of environmental conditions. Beamish (1978) and Randall and Brauner (1991) reviewed the impact of water temperature, salinity, dissolved gases and pollutants, upon aerobic swimming, primarily measured as  $U_{crit}$ . In particular, Randall and Brauner (1991) argued that the  $U_{crit}$  performance of salmonid species is impaired when environmental factors deviate from particular optimal values (Fig. 10.1). The current chapter will provide an update of knowledge upon how major abiotic environmental factors influence aerobic and  $U_{crit}$  performance, and will also review evidence that diet quality is an environmental factor that can significantly influence these elements of physiological performance.

## Temperature

Temperature is probably the most significant abiotic environmental factor for fish, with a controlling influence upon all aspects of their physiology and metabolism (Fry, 1947, 1971; Brett, 1971). It has a profound effect upon aerobic swimming performance that has been the subject of specific reviews, including with reference to potential effects of global warming (Taylor *et al.*, 1997; Farrell, 2007; Rome, 2007). The reader is advised to consult these and only a summary of the major effects of temperature is provided here.

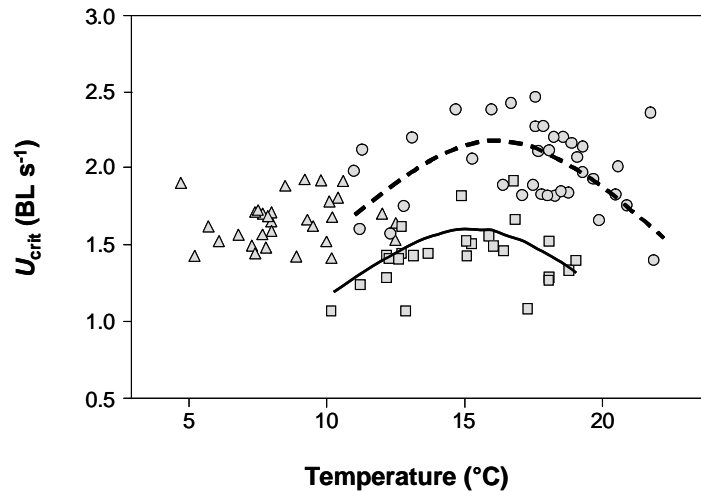
Brett (1971) and Brett and Glass (1973) demonstrated a unimodal bell-shaped relationship between temperature and  $U_{crit}$  performance in sockeye salmon (*Oncorhynchus nerka*), with low performance at the extremes of the species' temperature range, and a clear thermal optimum at which performance was maximal. There is good evidence to indicate that these temperature effects on  $U_{crit}$  reflect changes in aerobic performance, and the bell-shaped relationship is generally accepted as the typical effect of



**Fig. 10.1** Calculation used to determine critical swimming speed ( $U_{crit}$ ) (A), and the effect of water temperature (B), elevated plasma Na<sup>+</sup> concentration (C) and water pH (D) on  $U_{crit}$  performance in various salmonid species. BL, body length. Figure redrafted from Randall and Brauner 1991, with permission from the Company of Biologists.

temperature on maximum aerobic swimming performance in all fishes, with species-specific optima (see Beamish, 1978; Randall and Brauner, 1991, and Farrell, 2007, for reviews). Lee *et al.* (2003) demonstrated this bell-shaped relationship for adult sockeye and coho (*O. kisutch*) salmon migrating up the Fraser river (British Columbia, Canada), where different stocks exhibited temperature optima for maximum metabolic rate during swimming, aerobic metabolic scope, and  $U_{crit}$  that were very similar to the average ambient water temperatures of their natal streams (Fig. 10.2). This may indicate that thermal adaptation has occurred over an evolutionary time scale, although temperature sensitivity of performance was not particularly marked and the fish would retain at least 90% of their maximum aerobic performance over a range of temperatures spanning as much as 5°C. This would allow the fish to respond to annual variations in water temperature (Lee *et al.*, 2003; Farrell, 2007).

Temperature influences aerobic swimming performance by direct effects on muscle function (including myocardial function) and on metabolic rate and consequent O<sub>2</sub> demand. The relatively poor performance at low temperatures may result from an overall depression of all physiological



**Fig. 10.2** Relationships between critical swimming speed ( $U_{crit}$ ) and water temperature ( $t$ ) for different species and stocks of adult Pacific salmon captured during their migration up the Fraser River, Canada. Circles are the Gates Creek stock of sockeye (*Oncorhynchus nerka*) salmon, where the dotted line is  $U_{crit} = 2.17/1 + [(t-16.15)/9.59]^2$  ( $P < 0.05$ ;  $r^2 = 0.41$ ). Squares are Weaver Creek sockeye salmon, for which the solid line is  $U_{crit} = 1.60/1 + [(t-15.18)/8.52]^2$  ( $P < 0.05$ ;  $r^2 = 0.27$ ). The triangles are for Chehalis coho (*O. kisutch*) salmon, where there was no statistically significant relationship with temperature over the range examined. Data from Lee *et al.* 2003, with permission from the Company of Biologists.

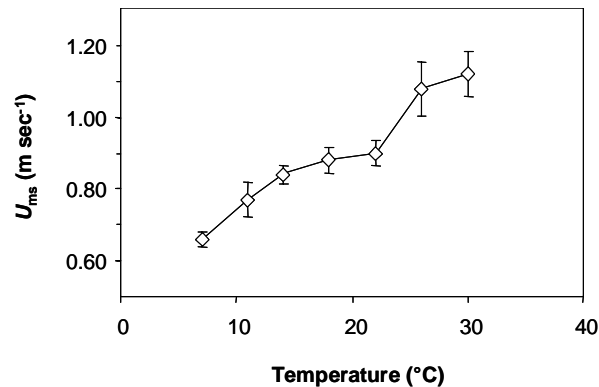
processes, but in particular of muscle function. Rome *et al.* (1984) demonstrated that the reduced swimming performance of carp (*Cyprinus carpio*) acclimated to cold water occurs because there is a compression of the speed range over which red and then white muscles are recruited, with early recruitment of white fibres at much lower swimming speeds. Working on swimming carp and scup (*Stenotomus chrysops*), Rome (1990) and Rome *et al.* (1992) demonstrated that temperature has a direct effect on the maximum velocity of shortening of muscle fibres and upon their maximum power production. The power production of red muscle is depressed at low temperatures and this requires the early recruitment of white fibres.

As temperature rises towards the optimum, positive effects on muscle function and associated power generation contribute to an increase in swimming performance (Temple and Johnston, 2002; Rome, 2007, for reviews). Claireaux *et al.* (2006) demonstrated, however, that the net cost of swimming was relatively stable in sea bass seasonally acclimated to temperatures beyond 11°C, increased swimming performance at higher temperatures was due to an increase in maximum aerobic metabolic rate and aerobic metabolic scope. That is, there was a tight relationship between these aerobic performance traits and maximum aerobic swimming speed ( $U_{ms}$ , defined as the maximum

swimming speed that the sea bass could achieve before exhibiting burst and coast swimming behaviours, Claireaux *et al.*, 2006). The authors suggested, therefore, that improved swimming capacity with increasing temperature resulted largely from increased energy fluxes and support metabolism, and therefore in scope for activity, rather than in properties of muscle function per se (Rome, 1990; Taylor *et al.*, 1997). However, there are some examples in the literature where swimming costs increased with water temperature. For instance, Dickson *et al.* (2002) found that the energetic costs of swimming at a given speed increased with temperature in chub mackerel *Scomber japonicus*, and McKenzie *et al.* (2007b) found similar results for the cyprinid chub, *Leuciscus cephalus*.

The reasons for the relative decline in aerobic performance as temperature exceeds the optimum are many. Firstly, because temperature increases all metabolic processes, it elicits an exponential increase in metabolic rate in fishes (Fry, 1971), both of maintenance metabolism and all other routine metabolic activities. There is not, however, a coincident increase in maximum aerobic metabolic rate because, presumably, of intrinsic constraints to maximum cardiorespiratory performance. As a result, as temperature increases, the demands for maintenance and routine activities rise inexorably towards the maximum possible rate, with a coincident decline in aerobic metabolic scope, until a lethal temperature where they coincide (Brett, 1971; Fry, 1971; Taylor *et al.*, 1997). The intrinsic constraints to maximum aerobic performance at high temperature have been discussed in detail before (Taylor *et al.*, 1997; Farrell, 2007) and may include diffusion limitations at the gills and an inability of the heart to meet the very elevated oxygen demands of the tissues. These same limitations presumably also underlie the lethal effects of the highest temperatures (Taylor *et al.*, 1997).

What is clear, however, is that the form of the bell-shaped temperature curve is strongly influenced by rates of temperature acclimation, being most pronounced in fishes that are exposed to acute temperature change, and increasingly less pronounced with time of acclimation. At low temperatures, muscle performance may improve with acclimation because of adaptive changes to the isomeric composition of ion channels in the sarcolemma, with the insertion of channels that work better at low temperatures (Temple and Johnston, 2002). Similar processes of molecular acclimation presumably also occur in the myocardium. The relative improvements to  $U_{crit}$  at higher temperatures will also reflect changes at this level but presumably also in organismal metabolic temperature adaptation, so that costs for maintenance metabolism and routine activities drop progressively as fish acclimate to the increased water temperature, and so the metabolic scope available for aerobic swimming is extended (Fry, 1971; Taylor *et al.*, 1997).



**Fig. 10.3** Maximum sustainable aerobic swimming speed ( $U_{ms}$ ) in European sea bass (*Dicentrarchus labrax*) seasonally acclimatised to seven water temperatures over an annual cycle encompassing their seasonal thermal range in the Bay of Biscay (Mid-Atlantic). Data are mean ( $\pm$  SEM) of at least 7 animals at each temperature, and are derived from Claireaux *et al.* (2006).

Relatively few studies have investigated the effect of seasonal thermal acclimatisation (rather than laboratory acclimation) on aerobic swimming performance in fish, and these have rarely measured the effects of more than three environmental temperatures (Butler *et al.*, 1992; Taylor *et al.*, 1996; Adams and Parson, 1998; Day and Butler, 2005; Claireaux *et al.*, 2006; McKenzie *et al.*, 2007b). Claireaux *et al.* (2006) measured  $U_{ms}$  in European sea bass, *Dicentrarchus labrax*, seasonally acclimatised to seven temperatures between 7°C and 30°C, these being the annual thermal range that they experience in coastal waters of the mid Atlantic (Bay of Biscay, France). As defined above,  $U_{ms}$  should be a true measure of maximum aerobic performance at the prevailing temperature. Claireaux *et al.* (2006) did not find a pronounced bell-shaped curve but, rather, swimming performance increased markedly with temperature from a minimum at 7°C up to about 22°C, beyond which performance levelled off, although the maximum was at 30°C (Fig. 10.3). This shows a remarkable ability of the sea bass to maintain performance over its natural thermal range, although it is to be presumed that temperatures higher than 30°C would eventually cause a decline in performance. Other studies have found little effect of temperature upon  $U_{crit}$  in fish that were seasonally acclimatised, indicating that some species may in fact be capable of almost perfect compensation of performance (Butler *et al.*, 1992; Taylor *et al.*, 1996; McKenzie *et al.*, 2007b). Interestingly, Day and Butler (2005) demonstrated that brown trout acclimated to reversed seasonal temperature displayed reduced  $U_{crit}$ , suggesting that factors other than temperature (the authors suggest photoperiod) contribute to seasonal compensation of performance.

A discussion of the effects of temperature on aerobic swimming in fishes would be incomplete without some mention of fish with regional endothermy, such as the tunas and lamnid sharks, which use vascular counter-current heat-exchangers (the *retia mirabilia* in tunas) to maintain their red muscle at temperatures above ambient. The comparative metabolism, energetics and performance of aerobic exercise in these fish groups have been the subject of in-depth reviews (Bernal *et al.*, 2001; Block *et al.*, 2001; Graham and Dickson, 2004), and shall only be given a brief mention here. Tunas perform continuous sustained aerobic exercise, to ram ventilate their gills and generate lift, and as part of a life history that involves constant foraging and wide-scale migrations. The red muscle is located in a different position to other fishes, being towards the centre of the body, and the heat produced by the continuous swimming activity is retained by the *rete* (see Graham and Dickson, 2001, for a review). Tunas are generally considered to be amongst the most powerful of all aerobic swimmers, and their exceptional sustained aerobic performance is at least in part due to increased power output and contraction rates in their warm red muscle (Graham and Dickson, 2001, 2004), coupled with an exceptional cardiac pumping capacity (Brill and Bushnell, 2001). Lamnid sharks show some interesting evolutionary convergences with the tunas, but have been relatively less well studied (see Bernal *et al.*, 2001, 2005; Donley *et al.*, 2004). Although these adaptations allow such animals to swim at relatively high sustained speeds throughout their lives, the few studies of tuna performance in a  $U_{crit}$  protocol have not revealed higher relative  $U_{crit}$  in bodylengths per second, than other large fish athletes, such as Chinook salmon (Lee *et al.*, 2003; Graham and Dickson, 2004). Furthermore, how water temperature influences aerobic swimming performance in fishes with regional endothermy remains to be described (e.g., Graham and Dickson, 2004). Bernal *et al.* (2005) reported that isolated red muscle fibres of the salmon shark, *Lamna ditropis*, were designed for high power production at very high body temperatures (26°C or above) only, and did not produce useful work and power below 20°C, only 6°C below their operating temperature *in vivo* but still over 10°C warmer than their ambient water.

It is clear that the effects of temperature on aerobic swimming performance may be of great ecological significance for fishes. They could be very profound if fish encounter sudden changes in water temperature, which may impede their capacity for sustained exercise. This may limit foraging behaviours but, most significantly, may impede migration in the vicinity of, for example, thermal power stations which use surface waters to cool their turbines. Furthermore, although many species are clearly able to acclimatise to the seasonal changes in temperature in their environment, there is some risk that the increased maximum summer temperatures which have accompanied overall global warming may exceed the adaptive range

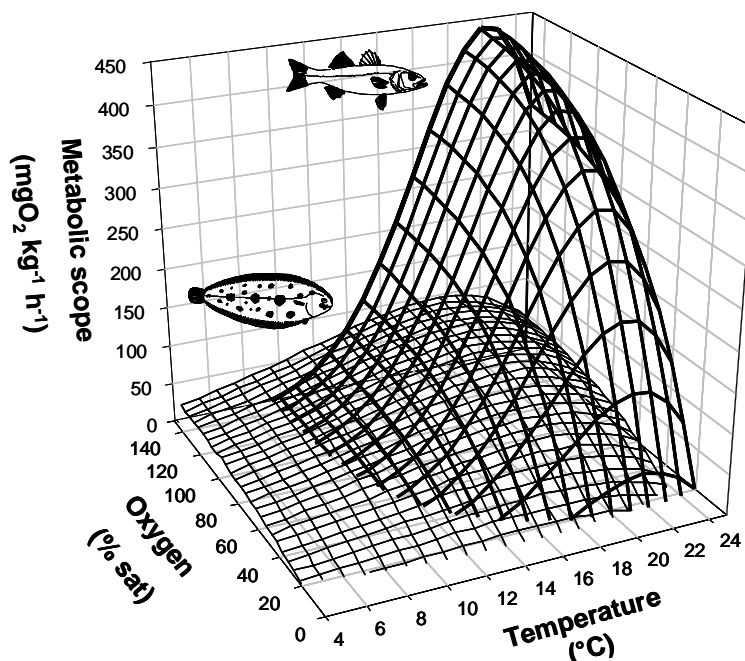
of some and so, potentially, modify their migratory cycles and behaviours (Taylor *et al.*, 1997; Lee *et al.*, 2003). One ecological effect that has already been observed, which must be linked to the performance of sustained aerobic exercise, is the change in distribution patterns of various marine species in response to global warming. This may be a facultative behavioural response of habitat selection, which has been experimentally demonstrated in species such as Atlantic cod, *Gadus morhua* (Claireaux *et al.*, 1995a). Some species may expand their range to colonise areas that were once too cold (Perry *et al.*, 2005; Hiddinck and ter Hofstede, 2008) whereas other may do the opposite, with increasing temperature constraining their distribution (Perry *et al.*, 2005). There is evidence that reductions in species range may be mediated by limitations to their aerobic metabolic scope (Pörtner and Knust, 2007).

### Dissolved O<sub>2</sub> and CO<sub>2</sub>

Water is intrinsically rather poor in dissolved O<sub>2</sub>, and this has long been recognised as the most important environmental factor limiting aerobic metabolic scope in fishes (Fry, 1947, 1971). Hypoxia occurs quite frequently in aquatic habitats, especially freshwater environments, when overall respiration rates exceed O<sub>2</sub> production by autotrophs and O<sub>2</sub> diffusion from the atmosphere. Hypoxic events due to anthropogenic eutrophication are now growing in frequency in aquatic habitats worldwide (see Diaz, 2001; Wu, 2002; Diaz *et al.*, 2004, for reviews).

Figure 10.4 demonstrates the limiting effect that hypoxia has on maximum aerobic metabolic rate in two species of marine teleost, the European sea bass and the common sole (*Solea solea*), seasonally acclimatised to a range of different temperatures (Claireaux and Lagardère, 1999; Lefrançois and Claireaux, 2003). Hypoxia has been shown to limit the performance of various species in the  $U_{crit}$  test (Davis *et al.*, 1963; Dahlberg *et al.*, 1968; Jones, 1971), in the rainbow trout this is coupled with the expected limitation to maximum aerobic metabolic rate and metabolic scope (Bushnell *et al.*, 1984). Dutil *et al.* (2007) found that the transition from steady swimming to burst and coast movements occurred at lowered speeds in Atlantic cod (*Gadus morhua*) swimming under hypoxic conditions compared to individuals in normoxia.

Presumably, the fish are limited in their ability to provide oxygen to the red muscles and, in turn, to their heart via the venous blood, so they resort to anaerobic swimming mode earlier and quit at lower swimming speeds in the  $U_{crit}$  test. Dahlberg *et al.* (1968) demonstrated interspecific diversity in sensitivity to the limiting effect of hypoxia, with largemouth bass (*Micropterus salmoides*) being less sensitive than Chinook salmon (*O. tshawytscha*), a difference which presumably parallels their overall hypoxia tolerance.



**Fig. 10.4** Surface plots of the interactive effects of water oxygen saturation (%) and water temperature upon the aerobic metabolic scope of two species of marine teleost, the European sea bass, *Dicentrarchus labrax*, (steep upper surface curve) and the Dover sole, *Solea solea* (shallow lower surface curve). Models derive from data reported in Claireaux and Lagardère (1999) and Lefrançois and Claireaux (2003).

Bushnell *et al.* (1984) found that acclimation of rainbow trout for two weeks to various levels of hypoxia did not improve their ability to perform aerobic exercise, indicating that this species might not be able to compensate for chronic environmental hypoxia, except perhaps on an evolutionary time scale.

Hypoxia can also influence the intensity of spontaneous aerobic swimming activity in fishes. In some species such as crucian carp, *Carassius carassius* (Nilsson *et al.*, 1994), Atlantic cod (Schurmann and Steffensen, 1994) and Adriatic sturgeon, *Acipenser naccarii* (McKenzie *et al.*, 1995), spontaneous aerobic swimming activity is reduced in hypoxia, presumably as an energy-saving response. In other species such as Atlantic herring, *Clupea harengus*, hypoxia causes increased activity, which presumably reflects a desire to escape and may involve both aerobic and anaerobic components (Domenici *et al.*, 2000; Herbert and Steffensen, 2006).

A number of teleost fish species have evolved the ability to gulp air at the water surface and store this in a variety of air-breathing organs (ABO), to then extract the O<sub>2</sub> (Graham, 1997). These adaptations for bimodal respiration (i.e., to breathe both water with gills and air with an ABO) are believed to



have evolved, at least in part, as a response to environmental hypoxia in tropical habitats (Randall *et al.*, 1981; Graham, 1997). Farmer and Jackson (1998) reported that the bowfin, *Amia calva*, a primitive bony fish which uses a modified swimbladder as an ABO, exhibits an exponential increase in air-breathing events when exposed to a step-wise  $U_{crit}$  protocol. There are also anecdotal reports that other fish with bimodal respiration use air-breathing during activity (reviewed in McKenzie *et al.*, 2007a) and thus it would be interesting to determine whether this allows them to avoid any negative effects of aquatic hypoxia on their aerobic exercise performance.

Aquatic hypoxia may have significant ecological implications for water-breathing fishes through its effects on aerobic swimming performance. Clearly, foraging and migratory performance may be limited if fishes encounter hypoxic areas. The behavioural responses to hypoxia may also have ecological implications, some species may reduce all activities that depend upon aerobic swimming until conditions improve, and other species may migrate away and change towards less hypoxic areas. Indeed, fish such as the Atlantic cod can show clear behavioural responses of habitat selection to avoid hypoxia (Claireaux *et al.*, 1995b).

The partial pressure of  $\text{CO}_2$  ( $\text{PCO}_2$ ) in surface waters is typically less than 0.015 kPa ( $\sim 1$ -mm Hg), but this can increase as a consequence of microbial metabolism and inadequate surface gas exchange, causing hypercapnia. There is now a growing interest in the potential effects on fish of the accumulation of  $\text{CO}_2$  in all aquatic habitats worldwide, which reflects the accumulation of this molecule in the atmosphere as a whole (Ishimatsu *et al.*, 2005). Fish, of course, produce  $\text{CO}_2$  from aerobic metabolism, which then diffuses across the gills into the surrounding water. Aquatic hypercapnia inhibits excretion, and can even cause  $\text{CO}_2$  to diffuse into the blood across the gills. This can cause the blood to become more acid and its  $\text{O}_2$ -carrying capacity to be reduced (reviewed by Heisler, 1984, 1993). Severe levels of hypercapnia may also cause acidosis of muscle and cardiac tissue, and impair their metabolism (Heisler, 1984, 1993; Driedzic and Gesser, 1994).

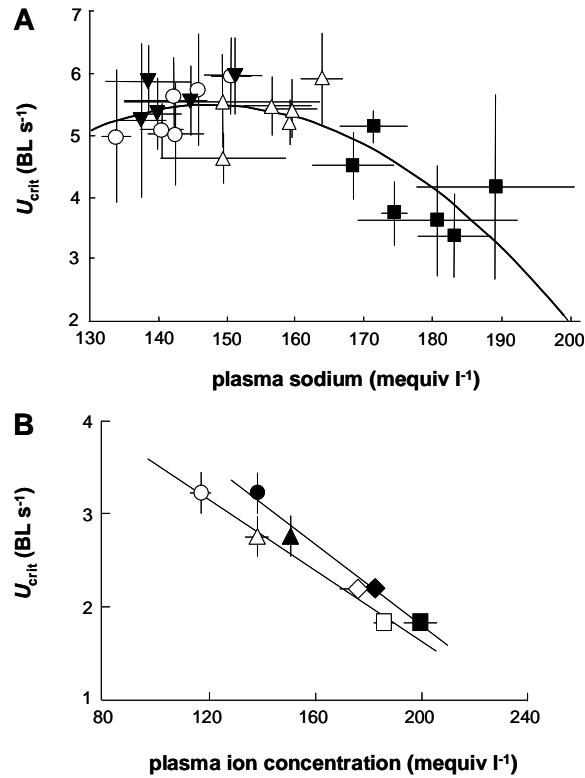
Dahlberg *et al.* (1968) demonstrated that acute exposure to hypercapnia, with no time given for acid-base compensation, limited  $U_{crit}$  performance in largemouth bass and Chinook salmon, with salmon being more sensitive than bass. McKenzie *et al.* (2003a) found, on the other hand, that chronic hypercapnia had no effect on the  $U_{crit}$  performance of European eels, *Anguilla anguilla*, despite a 50% reduction in  $\text{O}_2$  carrying capacity. Thus, this very limited database does nonetheless indicate that there are wide inter-specific differences in the effects of hypercapnia on  $U_{crit}$  performance in teleosts. The impaired  $U_{crit}$  performance in hypercapnic salmon and bass (Dahlberg *et al.*, 1968) may have reflected limitations to tissue  $\text{O}_2$  supply and/or direct

negative effects of extracellular and intracellular acidosis on the function of skeletal and cardiac muscle (Driedzic and Gesser, 1994).

Teleosts can compensate for hypercapnic acidosis, and consequent effects on blood O<sub>2</sub> carrying capacity and tissue intracellular pH, by ion-exchange at the gills, accumulating bicarbonate (HCO<sub>3</sub><sup>-</sup>) ions at the expense of an equimolar loss of chloride (Cl<sup>-</sup>), although there are species-specific limits to the extent to which this compensation can occur (Heisler, 1984, 1993; McKenzie *et al.*, 2003a). Thus, CO<sub>2</sub> accumulation in global waters worldwide may have significant ecological implications through effects on aerobic swimming performance (Ishimatsu *et al.*, 2005). In particular, if this accumulation exceeds the capacity for compensation of a species, it will have no means of escape and will exhibit permanently impaired scope to forage and migrate.

### Salinity

Many fish species swim through waters that differ markedly in salinity, some as an obligatory component of their spawning migrations (e.g., salmon, eel and sturgeon), and others as a facultative element of foraging strategies (e.g., sea bass, sea bream and mullet). A number of studies have shown a direct link between the ability to perform aerobic exercise and the homeostatic regulation of body fluid osmolality (Brauner *et al.*, 1992, 1994; McKenzie *et al.*, 2001a, b; Chatelier *et al.*, 2005). In coho salmon (*O. kisutch*) smolts, and Adriatic sturgeon juveniles, a “seawater challenge” comprising direct transfer from freshwater (at a salinity of 0‰) to seawater (28‰) caused a significant reduction in  $U_{crit}$  at 24 h later. This reduced performance was directly related to an accumulation of plasma ions and large increases in plasma osmolality (Brauner *et al.*, 1992, 1994; McKenzie *et al.*, 2001a,b; Fig. 10.5). It has been suggested that this was due to impaired cardiac and skeletal muscle function consequent to ionic imbalances and loss of tissue moisture, with additional strain upon the heart from haemoconcentration (Brauner *et al.*, 1992, 1994; McKenzie *et al.*, 2001a, b). These effects remain to be demonstrated. Acclimation of the Adriatic sturgeon to slightly hypertonic brackish water improved their ability to regulate iono-osmotic status following the salinity challenge and, consequently, improved their post-challenge  $U_{crit}$  (McKenzie *et al.*, 2001b). This indicates that a period spent in the brackish waters of estuaries would improve the ability of this sturgeon species to tolerate excursions into full strength seawater, although *A. naccarii* is not reported actually to colonise the marine environment for extended periods (Rochard *et al.*, 1992). No such beneficial effect of prior salinity acclimation has been demonstrated in salmon smolts of the genus *Oncorhynchus* (Morgan and Iwama, 1992), although these species inhabit the marine environment as they grow from smolts to maturity (Hoar, 1976).



**Fig. 10.5** **A.** Second-order regression of the relationship between mean ( $\pm$  SEM) plasma sodium at rest and subsequent mean ( $\pm$  SEM) critical swimming speed ( $U_{crit}$ ) in coho salmon (*Oncorhynchus kisutch*) parr. Fish derive from four experimental treatments: freshwater controls (closed triangles); at 24 h following abrupt transfer to seawater at 28 g l<sup>-1</sup> (closed squares), at 5 days following transfer to seawater at 28 g l<sup>-1</sup> (open triangles), and at 24 h following transfer back from seawater to freshwater (open circles).  $N$  = at least 5 per data point,  $r^2$  = 0.68. Figure reproduced from Brauner *et al.* (1992).

**B.** Least-squares linear regression analysis describing the relationship of mean ( $\pm$ SE)  $U_{crit}$  versus mean ( $\pm$ SE) Na<sup>+</sup> (open symbols) and Cl<sup>-</sup> (closed symbols) measured in the plasma of Adriatic sturgeon (*Acipenser naccarii*) following exercise to fatigue. When reading from left to right down the regression lines, the symbols circles represent a group raised in freshwater (circles), a group raised in brackish water at 11 g l<sup>-1</sup> (triangles), the brackish water group at 24 h following abrupt transfer to seawater at 28 g l<sup>-1</sup> (diamonds), and freshwater group following the same abrupt transfer (squares).  $N$  = at least 6 animals for each point. See McKenzie *et al.* (2001b) for further details. Figures reproduced with permission from the NRC Research Press.

Nelson *et al.* (1996) studied Atlantic cod populations from brackish water lakes (20 ‰) or the marine environment (38 ‰), and found that reciprocal acclimation to the two salinities had no effect on the  $U_{crit}$  of either population, although it increased variability in performance. The gulf killifish (*Fundulus*

*grandis*) is an estuarine species and Kolok and Sharkey (1997) found that killifish acclimated to freshwater had a significantly lower  $U_{crit}$  than fish maintained in brackish water at a salinity of 10‰, which the authors attributed to the osmotic stresses the animals suffered in freshwater. Chatelier *et al.* (2005) investigated the effects of direct transfer from sea water (35‰) to freshwater on European sea bass  $U_{crit}$  and associated cardiac performance. They found that the sea bass was able to maintain both elements of performance unchanged at 24 h following this transfer, and the same was true of a reciprocal transfer from fresh to sea water. This was linked to an exceptional ability of sea bass to regulate plasma osmotic homeostasis and tissue water balance in the face of sudden changes in ionic and osmotic gradients between water and body fluids. The mechanism by which the sea bass do this is unknown. Varsamos *et al.* (2002) also found that sea bass had an exceptional capacity for osmotic regulation, and suggested that this might reflect extremely plastic morphofunctional adaptations of mitochondria rich (“chloride”) cell populations in the gills. Thus, the sea bass exhibited a very different response to that observed in the salmon and sturgeon, but this ability would clearly allow them to protect their swimming ability while moving throughout estuaries, and between marine, brackish water and freshwater habitats (Pickett and Pawson, 1994). It would be interesting to investigate whether other species which perform facultative movements can also regulate iono-osmotic homeostasis and thereby protect exercise performance.

### Toxicants

The use of aerobic swimming performance as an indicator of the sub-lethal toxic effects of aquatic pollution was first proposed many years ago (Cairns, 1966; Sprague, 1971). Since then, studies have demonstrated that  $U_{crit}$  is impaired by pollutants such as low pH (Ye and Randall, 1989; Butler *et al.*, 1992), dissolved metals (e.g., Waiwood and Beamish, 1978; Wilson *et al.*, 1994; Beaumont *et al.*, 1995a, b, 2003; Alsop *et al.*, 1999; Pane *et al.*, 2004), ammonia (e.g., Shingles *et al.*, 2001; Wicks *et al.*, 2002; McKenzie *et al.*, 2003b), and various non-natural toxic organic chemicals such as organo-phosphate pesticides (Peterson, 1974), organo-chlorine fungicides (MacKinnon and Farrell, 1992; Nikl and Farrell, 1993; Wood *et al.*, 1996) and bleached kraft pulp-mill effluents (Howard, 1975; MacLeay and Brown, 1979). The majority of these studies were performed upon the rainbow trout.

Many of the pollutants cause direct damage to the gills if they exceed certain concentrations, and this leads to a decline in aerobic swimming performance by interfering with gas transfer and so limiting maximum aerobic metabolic rate (Nikl and Farrell, 1993; Pane *et al.*, 1994; Wood *et al.*, 1996). Some heavy metals such as aluminium and nickel can cause an elevation

of standard metabolic rate at concentrations that do not damage the gills, and this metabolic loading factor then reduces metabolic scope and hence  $U_{\text{crit}}$  (e.g., Wilson *et al.*, 1994; Pane *et al.*, 2004). In brown trout, *Salmo trutta*, exposure to sub-lethal concentrations of copper (in slightly acidic water, at pH 5) impairs  $U_{\text{crit}}$  performance by interfering with ammonia excretion, causing plasma ammonia accumulation (Beaumont *et al.*, 1995a, b). Zinc may have a similar mode of action in rainbow trout (Alsop *et al.*, 1999). The negative relationship between plasma ammonia concentration and  $U_{\text{crit}}$  in copper-exposed trout (Beaumont *et al.*, 1995a, b) is very similar to that observed in rainbow trout and brown trout exposed to ammonia alone (Shingles *et al.*, 2001; McKenzie *et al.*, 2003b). Beaumont *et al.* (2000a, b) demonstrated that the plasma ammonia accumulation caused a depolarization of white muscle, which then compromised its recruitment at the highest speeds (Beaumont *et al.*, 2003; McKenzie *et al.*, 2006). Thus, the toxic effects of ammonia accumulation on  $U_{\text{crit}}$  performance, whether from environmental ammonia pollution or effects of heavy metals on excretion of the metabolic waste product, are not actually an impairment of aerobic performance (Beaumont *et al.*, 2003; McKenzie *et al.*, 2006).

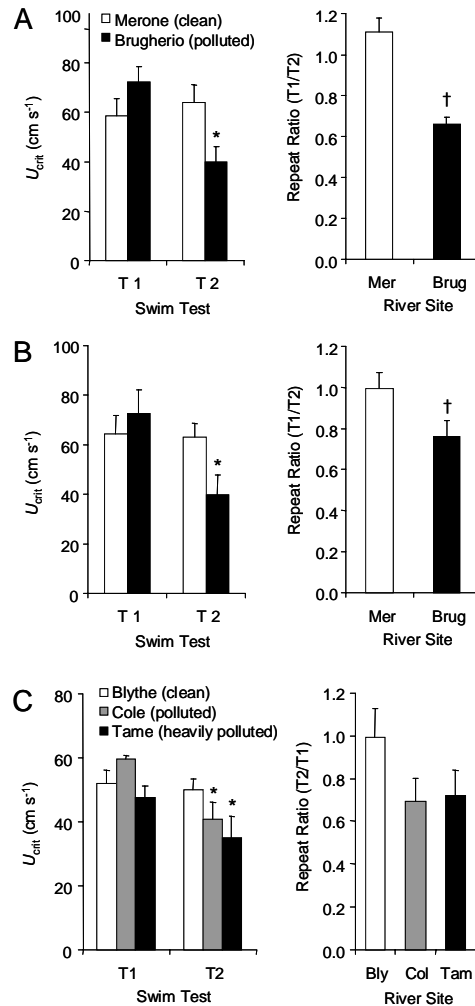
Clearly, the objective of ecotoxicological studies that investigate effects of pollutants on swimming performance is to establish ecologically relevant limits for pollutant concentrations in natural environments (e.g., MacKinnon and Farrell, 1992; Nikl and Farrell, 1993; Beaumont *et al.*, 1995a; Wicks *et al.*, 2002). The literature investigating the effects of pollutants upon fish exercise performance is, however, almost exclusively laboratory-based and, with few exceptions (Howard, 1975; MacLeay and Brown, 1979; Hopkins *et al.*, 2003; Taylor *et al.*, 2004), comprises the exposure of salmonid species to single toxicants. Very little is known about the potential physiological effects of exposure to polluted natural environments, which can contain a complex mixture of chemicals.

McKenzie *et al.* (2007b) investigated whether exposure to the mixtures of chemicals which prevail in polluted natural environments (urban rivers) had an impact upon the  $U_{\text{crit}}$  performance of two species of cyprinid fish, the chub and the carp. These are both lowland species characterising the “cyprinid reach”, where water flows are relatively slow and temperatures and  $O_2$  levels are often variable, even in the absence of pollution. Portable swimming respirometers were used to compare exercise performance and respiratory metabolism of fish exposed in cages for three weeks to either clean or polluted sites on three urban European river systems, in Italy, the UK and the Netherlands. Passive sampling devices were used to measure the bioavailable fraction of pollutants at the sites during the caging exposures. These analyses demonstrated that the polluted sites on the British and Italian rivers contained complex mixtures of bioavailable heavy metals and organics, whereas the Dutch river was severely polluted by mixtures of

bioavailable organics. Swimming performance was assessed with a “repeat-exercise” protocol, which measures the ability of fish to perform two sequential  $U_{crit}$  tests with a brief intervening recovery interval (Jain *et al.*, 1998). These authors demonstrated that rainbow trout can repeat  $U_{crit}$  performance perfectly after only 45 min recovery, with a “repeat ratio” of unity between first and second  $U_{crit}$  tests. Impairments to the second  $U_{crit}$  test proved to be a much more sensitive indicator of fish health and water quality than a single exercise test alone (Farrell *et al.*, 1998; Jain *et al.*, 1998).

In both Italy and the UK, indigenous chub exposed to clean or polluted sites swam equally well in the first  $U_{crit}$  test, but the chub from polluted sites could not repeat performance in the second test after a 45 min recovery interval (Fig. 10.6). This was due to impairments to their aerobic exercise performance, they were unable to raise metabolic rate and allocate oxygen towards exercise in the second trial. As a result, they exhibited significantly lower maximum aerobic metabolic rate and metabolic scope, and an approximately 30% reduction in  $U_{crit}$  with a repeat ratio of about 0.7. Similar results were obtained over two successive campaigns in Italy, and chub at the polluted sites in GB showed qualitatively similar responses (Fig. 10.6). Parallel studies on chub caged at the polluted sites demonstrated an accumulation of organics and metals that was directly related to the bioavailable fractions of these pollutants in the water (Winter *et al.*, 2004; Garofalo *et al.*, 2005). Thus, the impaired aerobic swimming performance could be linked to the increased bioavailable pollution at the sampling sites (McKenzie *et al.*, 2007b). The most likely explanation for this reduced performance in the second trial was impairments to the function of red and/or cardiac muscle (McKenzie *et al.*, 2007b), although extensive laboratory testing based upon the bioavailable pollutant mixtures prevailing at the sites would be necessary to verify this.

Exposure of cultured cloned carp to polluted sites on the Dutch river caused a marked accumulation of organic pollutants in their tissues (Verweij *et al.*, 2003) but did not, however, affect their repeat swimming performance (McKenzie *et al.*, 2007b). This may indicate either that the prevailing chemical mixture in this river was without effects on swimming performance, unlike the Italian and British rivers (which contained metals as well as organics), or that carp were more tolerant of the organic pollution. However, measurements of oxygen uptake during swimming revealed increased rates of routine aerobic metabolism in both chub and carp at polluted sites in all of the rivers studied, indicating a sub-lethal metabolic loading effect. It is not clear whether this metabolic loading was due to the presence of a particular pollutant or pollutant combination in the complex bioavailable mixtures in the rivers, because it can reflect an aspecific stress response in teleosts (Wendelaar Bonga, 1997). Seasonal studies on the chub in Italy and the UK also revealed that sub-lethal physiological effects of aquatic



**Fig. 10.6** Swimming performance of chub (*Leuciscus cephalus*) following exposure for three weeks in submerged cages to differently polluted sites on rivers in Italy or the United Kingdom. In each case, mean ( $\pm$  SEM) critical swimming speed ( $U_{crit}$ ) was measured twice, with the second swim test (T2) measured 40 min following fatigue in the first swim test (T1), to calculate the corresponding repeat performance ratio ( $U_{crit}$  T2/ $U_{crit}$  T1). Panels A and B show the effects of exposure of chub to two sites on the river Lambro near Milan: a relatively unpolluted site (Merone) or a polluted site (Brugherio), in June 2001 (A) and then in September 2001 (B). Panel C shows the effects of exposure of chub to one of three confluent rivers in Birmingham: the Blythe (unpolluted), the Cole (polluted) and the Tame (heavily polluted), in June 2002.  $n = 6$  in all cases, \* denotes a significant difference between T1 and T2 for that river site; † indicates a significant difference in repeat performance ratio between sites on the river Lambro. Bly, Blythe; Col, Cole; Tam, Tame. Data taken from McKenzie *et al.* (2007b) with permission from the Royal Society.

pollution were most obvious in fish acclimatised to warm spring/summer temperatures.

Therefore, the studies demonstrated that physiological traits of exercise performance and metabolic rate can indeed be used to reveal sub-lethal effects of aquatic pollution in natural environments. These physiological impairments may cause fish to be unable to colonise polluted areas successfully, in particular if seasonal spates and floods require them to perform repeated bouts of high-intensity aerobic exercise. Interestingly, many of the criteria required of biomarkers (Stegeman *et al.*, 1992; van der Oost *et al.*, 2003) are met by complex physiological traits of performance and metabolism such as the ability to repeat a  $U_{crit}$  swim test, and routine metabolic rate (McKenzie *et al.*, 2007b). Although they may be less specific than biochemical or molecular biomarkers, which can in theory reveal responses to specific pollutants (van der Oost *et al.*, 2003), and the exact mechanism by which exposure to polluted river sites caused the physiological impairments was not clear, these traits of aerobic metabolism are reliable integrated measures of the responses of many physiological systems, and can provide insight into why fish fail to colonise some polluted habitats. The physiological biomarkers may, therefore, be particularly useful within programs of ecological risk assessment which also comprise analyses of a suite of other biochemical and molecular markers.

### **Diet quality**

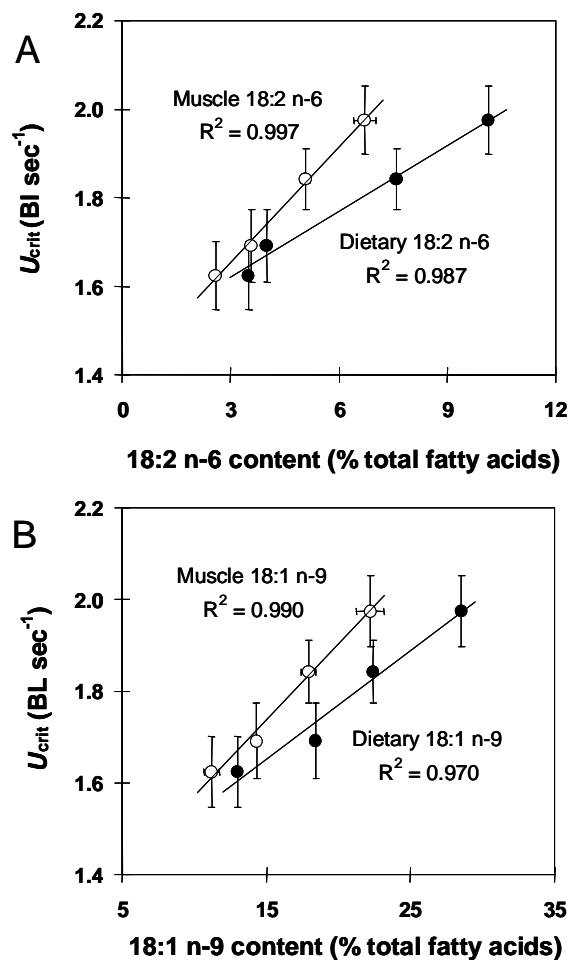
All animals interact profoundly with their environment through their diet, which provides all of the structural materials and energy required for expression of the phenotype. Diet is both an abiotic and a biotic factor, hence in a category unto itself. The interaction between animals and their environment through their diet is extremely complex, as revealed by the large number of “essential” nutrients that animals require in their food. The syndromes associated with deficiency in these compounds have been the focus of much research. There is also, however, a growing body of evidence to indicate that the relative intake of specific nutrients can have a profound effect on the physiology of well-nourished animals (Crawford and Marsh, 1989; Arts *et al.*, 2001; McKenzie, 2001, 2005), including upon their aerobic exercise performance (Beamish, 1988; McKenzie *et al.*, 1998; Wagner *et al.*, 2004; Chatelier *et al.*, 2006).

Beamish *et al.* (1988) investigated the potential effects of variation in dietary composition of major nutrient groups. They demonstrated that rearing lake trout (*Salvelinus namaycush*) on a protein-rich diet improved their  $U_{crit}$  swimming performance by comparison with conspecifics fed a lipid-rich or carbohydrate-rich diet. They attributed this to a larger muscle mass in the lake trout fed the protein-rich diet.



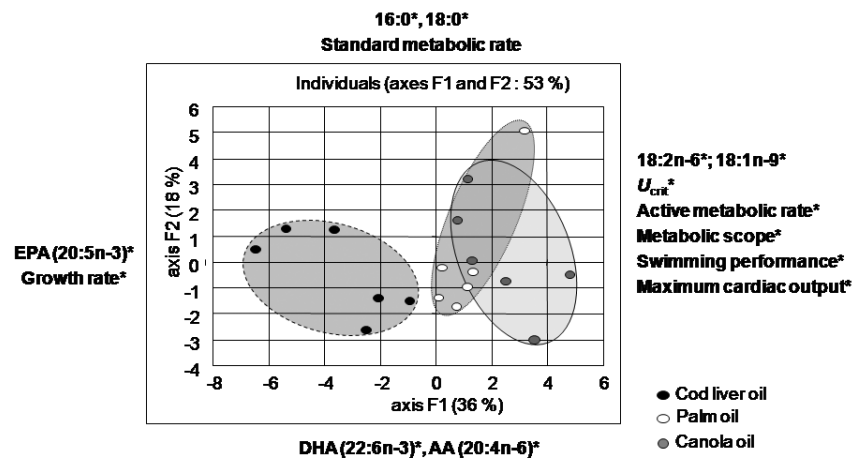
There has also been some interest in the relative dietary intake of certain fatty acids, in particular following the reports that long-chain highly unsaturated fatty acids of the n-3 and n-6 series have a major influence on human cardiovascular health (Bang and Dyerberg, 1985; British Nutrition Task Force, 1992) and also influence the respiratory and cardiovascular physiology of fishes (Bell *et al.*, 1991, 1993; Randall *et al.*, 1992). The long-chain highly unsaturated arachidonic acid (ARA, C20: 4n-6), eicosapentaenoic acid (EPA, C20: 5n-3), and docosahexaenoic acid (DHA, C22: 6n-3) are physiologically essential for the normal structure and function of cell membranes and are precursors of the autocrine eicosanoids (Sargent *et al.*, 1999). In all animals, the composition of fatty acids in the tissues reflects long-term intake in the diet, because the fatty acids are stored as fuels and also inserted into membrane phospholipids (hence the old axiom “we are what we eat”). Thus, studies can be performed to change tissue fatty acid composition by providing dietary lipids as specific natural oils, chosen for their relative composition of particular fatty acids (McKenzie *et al.* 2005). Marine fish oils are well-known to be rich in the essential fatty acids, especially EPA and DHA, whereas terrestrial plant oils can provide a spectrum of others (Sargent *et al.* 1999; McKenzie 2005).

Early work on the Adriatic sturgeon indicated that accumulation of EPA and DHA from dietary fish oil influenced metabolic rate and improved tolerance of hypoxia, both by the whole animal and the *in vitro* working heart (Randall *et al.*, 1992; McKenzie *et al.*, 1995; Agnisola *et al.*, 1996, reviewed in McKenzie, 2005). This led to an exploration of the potential positive effects of these essential fatty acids upon  $U_{crit}$  performance in Atlantic salmon, *Salmon salar* (Dosanjh *et al.*, 1998; McKenzie *et al.*, 1998). These studies investigated the effects of substituting dietary fish oil with increasing amounts of a vegetable oil (Dosanjh *et al.* 1998). It did not in fact reveal any positive effect of these fatty acids but, unexpectedly, revealed a direct positive relationship between  $U_{crit}$  and muscle levels of two unrelated ones, namely oleic acid (18: 1n-9) and linoleic acid (18: 2n-6) from the vegetable oil (McKenzie *et al.* 1998, Fig. 10.7). Chatelier *et al.* (2006) subsequently found that tissue accumulation of these same 18-carbon unsaturates from specific dietary vegetable oils improved the  $U_{crit}$  performance of European sea bass, and extended the observations to demonstrate that this was linked to improved maximum cardiac performance, higher maximum aerobic metabolic rate and greater metabolic scope (Fig. 10.8). The mechanistic basis for this effect on exercise and cardiac performance is unknown. It is known that aerobic metabolism, including work by red and cardiac muscle, is fuelled primarily by  $\beta$ -oxidation of fats in fish (Hochachka and Somero, 1984; Richards *et al.*, 2002), and there is *in vitro* evidence to suggest that, amongst the many fatty acids in the tissues, oleic and linoleic acids are preferred substrates for  $\beta$ -oxidation (Henderson and Sargent, 1985; Sidell and Driedzic, 1985;



**Fig. 10.7** Least squares linear regression analysis of the relationship between critical swimming speed ( $U_{crit}$ ) and the content of two fatty acids, (A) linoleic acid, 18: 2n-6 and (B) oleic acid, 18: 1 n-9, in the lipids of the muscle and the diet of Atlantic salmon (*Salmo salar*). Four groups of salmon had been fed one of four diets where the dietary lipid was composed of differing proportions of fish (menhaden) oil and vegetable (canola) oil. Open symbols, relation of mean ( $\pm$  SE) muscle % fatty acid (FA) content versus mean ( $\pm$  SE)  $U_{crit}$ ; closed symbols, mean dietary content versus mean ( $\pm$  SE)  $U_{crit}$ . N = 9 for muscle FA analyses, between 6 and seven for  $U_{crit}$ , 3 for dietary FA analyses. The group with the highest dietary and muscle content of these two FAs had a significantly higher  $U_{crit}$  than the group with the lowest levels. Modified from McKenzie *et al.* (1998) with permission from Elsevier.

Egginton, 1996). It is conceivable, therefore, that higher levels of these preferred substrates in the tissues might allow the animals to achieve higher rates of aerobic work (McKenzie, 2001, 2005). On the other hand, an interspecific study has demonstrated a positive relationship between skeletal



**Fig. 10.8** Principal components analysis (PCA) of the relationships between the content of particular fatty acids in the heart of individual European sea bass (*Dicentrarchus labrax*) and their measured values for various physiological traits, including critical swimming speed ( $U_{crit}$ ) and associated traits of cardiorespiratory performance. Three groups of sea bass had been fed one of three diets where the dietary lipid was provided as either fish (cod liver) oil, or one of two vegetable oils (palm or canola). The asterisks next to the variables on the PCA axes indicate where the mean values differed between the cod liver oil and vegetable oil groups by one-way analysis of variance. Data are taken from Chatelier *et al.* (2006).

muscle content of linoleic acid and running speed in terrestrial vertebrates, and has proposed that this is due to an effect of this fatty acid on the activity of the sarcoplasmic  $\text{Ca}^{2+}\text{Mg}^{2+}$ -ATPase (Ruf *et al.*, 2006). This remains an interesting area for future research.

McKenzie *et al.* (1998) and Chatelier *et al.* (2006) found that accumulation of EPA and DHA was associated with relatively poor exercise performance. These results are, however, in direct contrast to those reported by Wagner *et al.* (2004), who found improved  $U_{crit}$  performance in Atlantic salmon fed fish oils rich in these n-3 fatty acids. The explanation for these opposing results presumably lies in the enormous complexity of factors within such diet studies. In particular, because many of the fatty acids have specific biological roles that interact with each other, and the dietary fatty acids are provided as a complex mixture in natural oils (Sargent *et al.*, 1999). Thus, diet studies are very complex to interpret and each study is effectively unique unless great care is taken to match the ingredients. There may also be minimum threshold of action for some fatty acids (Chatelier *et al.*, 2006).

There is greater variation in tissue fatty acid phenotype within wild fish populations, including for EPA, DHA, oleic and linoleic acids (e.g., Jangaard *et al.*, 1967; Klungsøyr *et al.*, 1989; Kuusipalo and Käkälä, 2000; Budge *et al.*, 2002; Iverson *et al.*, 2002), than those associated with the differences in exercise performance described by McKenzie *et al.* (1998), Wagner *et al.*

(2004) and Chatelier *et al.* (2006). If such diversity in phenotype of wild fish is associated with diversity in physiological traits similar to that observed in the laboratory studies, then dietary fatty acid intake may have significant ecological implications. Many coastal marine species can exploit lagoons and estuaries during their life cycle, in which foodwebs can have larger inputs of fatty acids from terrestrial sources, hence richer in oleic and linoleic acids (Galois *et al.*, 1996). This diet may, therefore, contribute to their aerobic swimming performance. Diversities in dietary and tissue fatty acid composition within populations may contribute in some way to their overall physiological diversity, and so influence their responses to other environmental factors, such as temperature and hypoxia.

## CONCLUSIONS AND PERSPECTIVES

This review demonstrates quite clearly that the aerobic swimming performance of fishes (in particular as measured within the context of the  $U_{crit}$  protocol) is profoundly influenced by all of the most important environmental factors, namely water temperature, dissolved  $O_2$  and  $CO_2$ , salinity, toxicant load, and also by the chemistry of their diet. Clearly, the effects of these environmental factors on aerobic performance could influence such behaviours as searching for food, migrating and searching for mates.

The actual ecological significance of maximal aerobic exercise capacity remains, however, to be demonstrated, and very few studies have explored the relationship between aerobic swimming performance and fitness in natural populations (Billerbeck *et al.*, 2001; Lankford *et al.*, 2001). Nonetheless, Nelson and Claireaux (2005) and Claireaux *et al.* (2007) reported that  $U_{crit}$  was repeatable and stable over a significant portion of the lifespan of a European sea bass, such that the underlying traits of aerobic performance might indeed be potential targets for natural selection (Endler, 1986; Dohm, 2002). Thus, the major challenge for the future is to demonstrate the intuitive links between aerobic swimming and fitness.

Over the last 20–30 years, biologists have increasingly been solicited to provide legislators and conservation managers with information about the causal mechanisms underlying, for instance, a decline in biodiversity or the collapse of a population. This is particularly true for the world fishing industry, where there is an urgent need for reliable models for the sustainable management of aquatic resources. Mechanistic ecophysiology could play a critical role in integrated approaches to ecosystem management, by contributing to predictive models of how the environment influences the physiology of its inhabitants, and how this influences the fitness of their populations.

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