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Effect of temperature on maximum swimming speed and cost of transport in juvenile European sea bass (*Dicentrarchus labrax*)

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Summary

This study is an attempt to gain an integrated understanding of the interactions between temperature, locomotion activity and metabolism in the European sea bass (*Dicentrarchus labrax*). To our knowledge this study is among the few that have investigated the influence of the seasonal changes in water temperature on swimming performance in fish. Using a Brett-type swim-tunnel respirometer the relationship between oxygen consumption and swimming speed was determined in fish acclimatised to 7, 11, 14, 18, 22, 26 and 30°C. The corresponding maximum swimming speed (U_{max}), optimal swimming speed (U_{opt}), active (AMR) and standard (SMR) metabolic rates as well as aerobic metabolic scope (MS) were calculated. Using simple mathematical functions, these parameters were modelled as a function of water temperature and swimming speed. Both SMR and AMR were positively related to water temperature up to 24°C. Above 24°C SMR and AMR levelled off and MS tended to decrease. We found a tight relationship between AMR and U_{max} and observed that raising the temperature increased AMR and increased swimming ability. However, although fish swam faster at high temperature, the net cost of transport (COT_{net}) at a given speed was not influence by the elevation of the water temperature. Although U_{opt} doubled between 7°C and 30°C (from 0.3 to 0.6 m s^{-1}), metabolic rate at U_{opt} represented a relatively constant fraction of the animal active metabolic rate (40–45%). A proposed model integrates the effects of water temperature on the interaction between metabolism and swimming performance. In particular the controlling effect of temperature on AMR is shown to be the key factor limiting maximal swimming speed of sea bass.

Key words: swimming, cost of transport, metabolism, temperature, sea bass, modelling.

Introduction

Many fish in natural water bodies are subjected to large diurnal or seasonal changes in temperature. Consequently, these organisms have developed a wide range of regulatory mechanisms aimed at preserving overall performance at a wide range of body temperatures.

The ability to move is a fundamental property of animal life. Many factors, such as predator–prey interaction, reproductive behaviour and habitat selection, are of profound ecological importance and depend heavily on an animal's capacity for movement (Baker, 1978). Although rarely proven, intuitive logic would dictate that the ability to swim factors into Darwinian fitness (Arnold, 1983; Nelson, 1989). Despite this intuitive link to fitness, and despite the large number of studies conducted to date, the impact of water temperature on locomotor performance in fish still remains poorly described. This lack of understanding results mainly from the diversity of physical, biochemical, physiological and behavioural processes that are involved, and which interact at various organisational levels. In two reviews (Johnston and Ball, 1996; Taylor et al., 1997), a series of missing or incomplete pieces of information that prevent us from making adequate predictions regarding the effects of temperature on swimming performance were identified. These include the linkage between muscle work and swimming speed, the nature of the functional limits to swimming (see also Kieffer, 2000), the factors controlling swimming performance, the effect of acclimation *versus* acclimatisation (Butler et al., 1992), and phenotypic plasticity (see also Johnston and Temple, 2002). Moreover, although generally recognised, the multifaceted environmental influence on fish swimming ability remains insufficiently understood. For instance, Day and Butler compared the swimming ability of brown trout (*Salmo trutta*) acclimatised to seasonal temperature to that of individuals acclimated to reversed seasonal temperature (Day and Butler, 2005). They demonstrated that in the latter case full thermal compensation does not occur. They suggested that swimming abilities are influenced by seasonal factors other than temperature, possibly photoperiod (see also Kolok, 1991).

Sea bass are active pelagic fish that occupy estuarine marine waters as adults. They capture prey by pursuit, usually as part of a shoal when they are juveniles. In addition, adult sea bass undergo substantial annual migrations between coastal and offshore marine waters. Both juveniles and adults have been observed holding station in strong tidal currents and are subject to predation by marine mammals, pelagic fishes and several types of birds (Pickett and Pawson, 1994). Some degree of swimming performance is undoubtedly critical to the success of individual sea bass (*Dicentrarchus labrax*). Therefore, understanding the factors that control swimming performance should be important in predicting a sea bass's chances of survival in its natural environment. Management of the sea bass fishery in Europe is currently based on a package of technical measures designed to protect juveniles and to improve recruitment into the adult spawning stock. These measures are based on knowledge of the distribution of the various life history stages, their growth, and interactions with capture fisheries around the coasts of Europe (Pickett and Pawson, 1994). This information is important for understanding the relationship between adult biomass and ensuing recruitment. However, knowledge of biological factors that contribute to the recruitment into the reproducing population could vastly improve management models and should be an important element of any ecosystem approach to fisheries management. In the case of sea bass, the deficiency in basic information is striking, particularly when it comes to defining environmental tolerances and physiological optima. In recent years a progressive northward spread of sea bass has been recorded along the western coasts of Europe; this expansion is believed to be related to the warming of the European Atlantic waters (Quéro, 1998; Quéro et al., 1998; O'Brien et al., 2000; Stebbing et al., 2002). As the northern limits to the ranges of the species extend further, the effect on the fisheries is likely to be important but remains very difficult to predict.

With this deficit of information as a background, the present experiment was designed to investigate the effect of temperature on the relationship between aerobic metabolism and swimming performance in acclimatised European sea bass. In order to improve our ability to predict the effect of water temperature on that relationship, locomotion and associated metabolic performance were examined in seasonally acclimatised individuals. Our objectives were: (1) to establish the link between active metabolic rate and maximum swimming speed, (2) to model the controlling effect of temperature on the cost of swimming and (3) to propose an integrated description of the interactions between temperature, metabolism and swimming performance in sea bass.

Materials and methods

Fish collection and maintenance

Juvenile sea bass *Dicentrarchus labrax* Linnaeus 1758 of both sexes (mass 147.16±2.68 g; mean ± s.e.m.; range 105–248 g) were obtained from a local hatchery (Ferme Marine des Baleines, Ile de Ré, France). Upon arrival at the laboratory they were transferred into 500 litre indoor tanks supplied with recirculated and filtered natural seawater (water renewal rate: 30–50% per week). Fish were kept under natural photoperiod and temperature conditions and were fed twice a week on commercial dry pellets (2–4% of body mass). Experiments started 2 months after fish arrived in the laboratory. Feeding was discontinued 24 h before any manipulation of the animals and 3–5 days ahead of any oxygen consumption measurement.

Respirometer

A Brett-type swimming tunnel respirometer (39 litre) (Brett, 1964) was used to measure fish oxygen consumption rate ($\dot{M}_{O_2}$) as a function of swimming speed (U). The working section of the tunnel was 60 cm in length and 11.5 cm in diameter. A screen darkening the upstream section of the swimming chamber motivated the fish to occupy an upstream position. Water temperature in the respirometer was controlled within ±0.2°C with a Hubber (Offenburg, Germany) chilling unit connected to a titanium heat exchanger. A variable-speed pump propelled the water at a constant velocity. Plastic honeycomb and deflectors were inserted in the recirculation loop to promote rectilinear flow and a uniform velocity profile. Flow characteristics were visually assessed with dye flow patterns. A flow meter (Marsh-McBirney 200, Frederick, MA, USA) mounted in the centre of the swimming chamber was used to calibrate water velocity to voltage output from the pump controller. Swimming speeds were corrected for solid blocking effects using a procedure derived from Bell and Terhune (Bell and Terhune, 1970):

$$V_F = V_T\,(1 + \epsilon_s)\,, \qquad (1)$$

where V_F is the effective water velocity, V_T is the average water velocity in the empty swimming section and ϵ_s is the fractional error in V_T due to blockage. ϵ_s was calculated as follows:

$$\epsilon_s = \tau\lambda(A_o/A_t)^{3/2}\,, \qquad (2)$$

with τ a dimensionless factor depending on the tunnel cross-sectional shape (0.8), λ a shape factor for the fish [0.53(length/thickness)], A_o the cross-sectional area of the fish and A_t the cross-sectional area of the swim chamber.

Water oxygen concentration was recorded continuously using an Orbisphere Laboratories (Neuchâtel, Switzerland) oxygen meter (2610) and probe (27141) interfaced to a computer. In open mode, the respirometer was supplied with fully aerated and thermoregulated seawater that circulated to a reservoir tank at a flow rate of 4–5 l min^{-1}. In closed mode, fish $\dot{M}_{O_2}$ was calculated from the rate of oxygen depletion according to the equation:

$$\dot{M}_{O_2} = \text{slope}\ VOL_{\text{resp}}\, M_b^{-1}\,, \qquad (3)$$

where $\dot{M}_{O_2}$ (mmol kg^{-1} h^{-1}) is oxygen consumption, slope (mmol h^{-1}) is the decrease in water oxygen content per unit time, VOL_{resp} (l) is the volume of the respirometer minus the volume of the fish, and M_{b} (kg) is the mass of the fish.

The level of oxygen saturation in the respirometer was never allowed to fall below 85%. $\dot{M}_{\mathrm{O2}}$ values resulting from a regression with a $r^2<0.95$ were not considered in the analysis. Oxygen consumption measurements were adjusted to a standard body mass of 100 g using a mass exponent of 0.77 (Herskin and Steffensen, 1998). Prior to each experimental run, the oxygen probe was calibrated in air-saturated water.

Experimental protocol

Experiments took place from December 1999 to June 2001, on fish seasonally acclimatised to the environmental temperature prevailing in their rearing facility. At each experimental temperature (7, 11, 14, 18, 22, 26 and 30°C) 7–10 fish were transferred to a 500 litre tank situated in a thermoregulated room, with a photoperiod matched to the natural seasonal hours of daylight and darkness. The temperature difference between the two rearing facilities never exceeded 0.5°C. After 12–18 days (experimental temperature, salinity 25%–28‰), during which they were fed regularly, animals were sequentially anaesthetised (2-phenoxyethanol; dilution 0.3 ml $\mathrm{l^{-1}}$), weighed, and their length, width and depth measured. Fish were then placed in the respirometer and left undisturbed overnight at a water velocity of 10 cm $\mathrm{s^{-1}}$.

Each experimental run consisted of a 30 min period at each of the designated speeds up to the maximum speed. The speed increment was 10 cm $\mathrm{s^{-1}}$, with the speed raised at a rate of 4 cm $\mathrm{s^{-1}}$ $\mathrm{min^{-1}}$. At each speed, fish $\dot{M}_{\mathrm{O2}}$ was calculated using the last 15 min of a 30 min $\mathrm{O_2}$ monitoring period. After each run the fish was removed from the swimming chamber and the respirometer was re-sealed for determination of background $\dot{M}_{\mathrm{O2}}$ by micro-organisms, which was then subtracted from fish $\dot{M}_{\mathrm{O2}}$ measurements. Between experimental runs the entire apparatus was cleaned using a chlorine bleach solution, flushed repeatedly and refilled with seawater.

Maximum swimming speed

The maximum swimming speed (U_{max}) that fish were able to attain was determined by direct observation. The criteria that we used to define U_{max} were similar to those used by Sepulveda and Dickson (Sepulveda and Dickson, 2000), i.e. fish generally displayed burst-and-glide swimming mode and $\dot{M}_{\mathrm{O2}}$ usually levelled off or decreased slightly (Tang et al., 1994; Drucker, 1996; Sepulveda and Dickson, 2000; Peake and Farrell, 2004).

Standard metabolic rate and active metabolic rate

For each temperature trial, an exponential regression equation was fitted by least squares to the $\dot{M}_{\mathrm{O2}}$ *versus* swimming speed (U) relationships:

$$\dot{M}_{\mathrm{O2}} = \mathrm{a} + \mathrm{b}U^{\mathrm{c}}\,, \tag{4}$$

where a, b and c are constants.

Standard metabolic rate (SMR) was determined by extrapolating the corresponding $\dot{M}_{\mathrm{O2}}$ *versus* swimming speed relationship to zero swimming speed. The metabolic rate associated with U_{max} was defined as the active metabolic rate (AMR). After transforming Eqn 4, the optimal swimming speed (U_{opt}) was calculated according to the following equation (Videler, 1993):

$$U_{\mathrm{opt}} = [\mathrm{a}/(\mathrm{c}-1)\mathrm{b}]^{1/\mathrm{c}}\,, \tag{5}$$

where the optimal swimming speed is the speed that minimises that the energy expenditure per unit of travel distance.

Swimming efficiency

The cost of transport (COT, in J $\mathrm{km^{-1}}$ $\mathrm{kg^{-1}}$) provides an index of overall swimming efficiency; the lower the COT value, the more efficient the locomotion. At each experimental temperature, $\dot{M}_{\mathrm{O2}}$ values were converted to J $\mathrm{km^{-1}}$ $\mathrm{kg^{-1}}$ using an oxycalorific equivalent [3.24 cal mg $\mathrm{O_2}$ (Beamish, 1978)] and converting cal to J (4.18 J $\mathrm{cal^{-1}}$). The obtained values were divided by the corresponding speed to obtain cost of transport. The relationship between COT and swimming speed was plotted and an exponential regression was fitted using the following equation (Videler, 1993):

$$\mathrm{COT} = \mathrm{a}/U + \mathrm{b}U^{(\mathrm{c}-1)}\,. \tag{6}$$

When plotted in relation to U, COT is a J-shaped function. As swimming speed increases, the initial decline of COT is due to a decrease in the relative contribution of SMR to the overall metabolic demand. At U_{opt}, COT reaches a minimum and thereafter increases as $\dot{M}_{\mathrm{O2}}$ rises with U. In order to avoid the temperature-mediated interaction between U_{opt} and SMR, we calculated the net metabolic demand ($\dot{M}_{\mathrm{O2net}}$) by subtracting the corresponding SMR from all $\dot{M}_{\mathrm{O2}}$ measurements. The net cost of transport ($\mathrm{COT_{net}}$, in J $\mathrm{km^{-1}}$ $\mathrm{kg^{-1}}$) was calculated according to the following equation (Videler, 1993):

$$\mathrm{COT_{net}} = E_{\mathrm{net}}\,/\,U\,, \tag{7}$$

where E_{net}, in J $\mathrm{h^{-1}}$ $\mathrm{kg^{-1}}$, is the energy expenditure corresponding to $\dot{M}_{\mathrm{O2net}}$ and U is in km $\mathrm{h^{-1}}$. Values of $\mathrm{COT_{net}}$ were then plotted in relation to U and a regression was fitted using the following equation:

$$\mathrm{COT_{net}} = \mathrm{b}U^{(\mathrm{c}-1)}. \tag{8}$$

Statistical analysis and modelling procedure

U_{max}, SMR and AMR measures were examined for normality and homogeneity of variance using Kolmogorov–Smirnov and F_{max} tests, respectively. No transformation was applied prior to analysis. U_{max}, SMR and AMR data were analysed *via* an ANOVA with water temperature being used as main factor. *A posteriori t*-tests for comparison of means with $\alpha=0.05$ were applied following ANOVA (Sokal and Rohlf, 1981). In order to combine the effects of temperature and swimming speed on metabolic rate the following modelling procedure was applied. The temperature-dependence of the parameters a, b and c (Eqn 4) were examined via regression analysis. The resulting functions

Table 1. *Influence of acclimatisation temperature on sea bass standard metabolic rate, active metabolic rate and maximum swimming speed*

T (°C)	*N*	SMR (mmol h^{-1} kg^{-1})	AMR (mmol h^{-1} kg^{-1})	U_{max} (m s^{-1})
7	5	1.38 ± 0.32^{a}	6.17 ± 0.52^{a}	0.67 ± 0.01^{a}
11	8	1.68 ± 0.09^{a}	7.01 ± 1.35^{a}	$0.77\pm0.03^{a,b}$
14	10	2.96 ± 0.17^{b}	$9.03\pm1.59^{a,b}$	$0.84\pm0.02^{b,c}$
18	9	2.87 ± 0.23^{b}	$10.56\pm0.81^{a,b}$	0.88 ± 0.02^{c}
22	10	$3.66\pm0.29^{b,c}$	12.75 ± 1.35^{b}	0.90 ± 0.02^{c}
26	8	4.47 ± 0.29^{c}	17.27 ± 1.23^{c}	1.08 ± 0.04^{d}
30	7	4.72 ± 0.26^{c}	19.05 ± 1.20^{c}	1.12 ± 0.04^{d}

T, acclimatisation temperature; U_{max}, maximum swimming speed; SMR, standard metabolic rate; AMR, active metabolic rate.

Values are means ± s.e.m.; *N*, number of individuals. In each column, numbers sharing a superscripted letter are statistically similar (*a posteriori t*-tests; $P<0.05$).

$a=f(T)$, $b=f'(T)$ and $c=f''(T)$ were then merged in Eqn 4 in order to draft a three-dimensional model:

$$\dot{M}_{O_2} = f(T) + f'(T)U^{f''(T)} \,. \qquad (9)$$

Throughout the manuscript, data are presented as mean ± 1 s.e.m. In all statistical analysis, $P<0.05$ was taken as the fiducial level for significance.

Results

Metabolic rates and maximum swimming speed

Sea bass maximum swimming speed (U_{max}), active metabolic rate (AMR) and standard metabolic rate (SMR) increased significantly with acclimisation temperature (ANOVA, $P<0.0001$; Table 1). Over the whole temperature range tested, the calculated Q_{10} values were 1.25, 1.63 and 1.71 for U_{max}, AMR and SMR, respectively. When the seven temperature trials were compared, a strong positive relationship between active metabolic rate and maximum swimming speed was observed (Fig. 1).

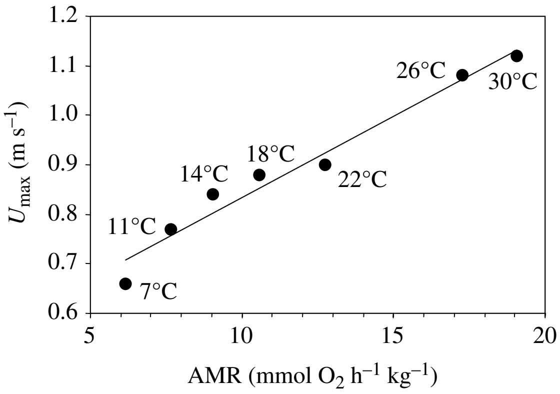

Fig. 1. Relationship between active metabolic rate (AMR*)* and maximal swimming speed (U_{max}) at various temperatures. Solid line: AMR=$0.033U_{max}+0.5051$ ($r^2=0.97$).

Energetics

At each experimental temperature a relationship between oxygen consumption (mmol h^{-1} kg^{-1}) and swimming speed (cm s^{-1}) was fitted by the least squares using Eqn 4 (Fig. 2). The values of the corresponding constants and r^2 are reported in Table 2. The effect of acclimatisation temperature on the relationship between swimming speed (*U*) and cost of transport (COT) was examined using Eqn 6 (Fig. 3) using the appropriate values for a, b and c given in Table 2. The optimal swimming speed (U_{opt}), $\dot{M}_{O_2}$ at U_{opt} and COT at U_{opt} were also calculated (Table 2). Values of $\dot{M}_{O_2}$ at U_{opt} increased with temperature ($r^2=0.93$; $P<0.01$) but always represented 44.5±2.45% of AMR at the temperature under consideration.

The relationship between swimming speed and net cost of transport (COT_{net}) showed that the cost of swimming at a given speed was not influenced by acclimatisation temperature (Fig. 4).

Modelling

In order to investigate the effect of seasonal temperature changes on the relationship between aerobic metabolism and swimming performance we designed a model on the basis of

Table 2. *Regression equations and* r^2 *values for the plots of oxygen consumption versus swimming speed using Eqn 4*

T (°C)	a	b	c	r^2	U_{opt} (cm s^{-1})	$\dot{M}_{O_2}$ at U_{opt} (mmol h^{-1} kg^{-1})	COT at U_{opt} (J kg^{-1} km^{-1})	COT_{net} at U_{opt} (J kg^{-1} km^{-1})
7	1.23	11.90	2.08	0.70	0.32	2.37	881.19	271.45
11	1.59	12.15	2.23	0.69	0.37	2.88	947.28	323.91
14	3.36	12.47	3.24	0.69	0.52	4.86	1123.90	536.86
18	2.76	8.35	1.95	0.62	0.58	5.67	1171.64	631.08
22	3.40	12.04	2.57	0.72	0.51	5.57	1306.43	526.56
26	4.35	11.21	2.74	0.86	0.58	6.59	1424.04	625.24
30	4.85	11.95	2.26	0.86	0.61	8.70	1727.92	668.56

$\dot{M}_{O_2}=a+bU^{c}$. *T*, temperature; U_{opt}, optimal swimming speed (Eqn 5).

$\dot{M}_{O_2}$ at U_{opt} and COT at U_{opt} were calculated using Eqn 4 and Eqn 6 and parameter values from Table 2. COT_{net} at U_{opt} were calculated using Eqn 11.

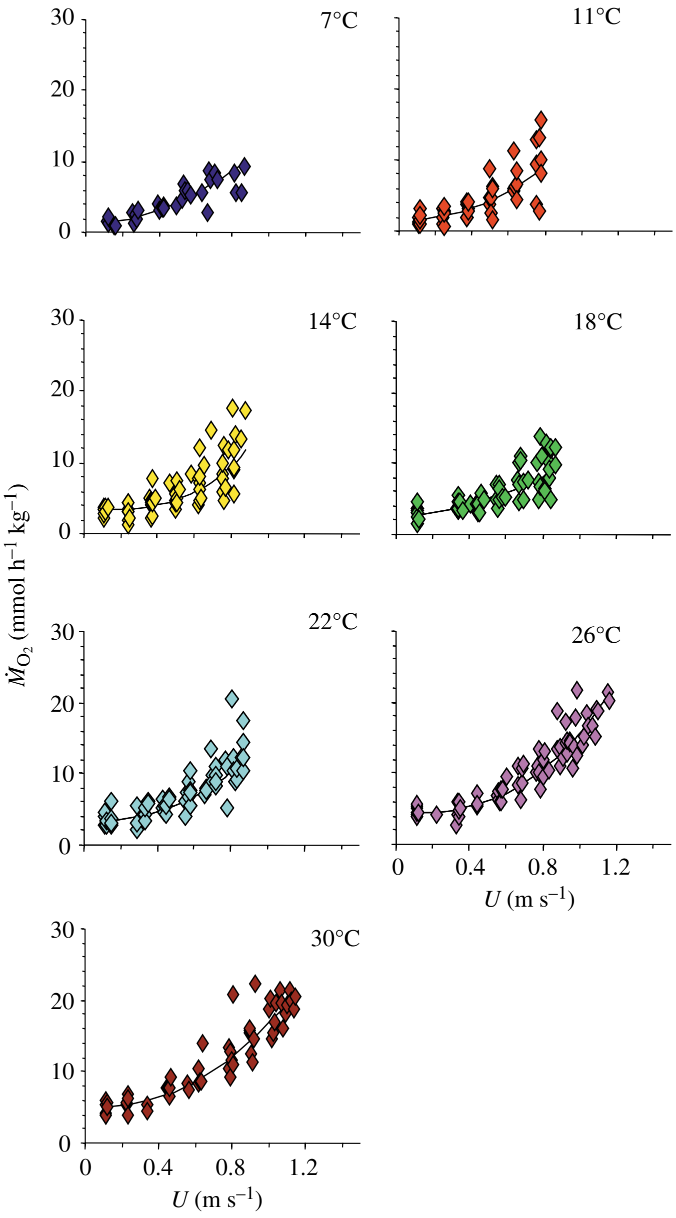

Fig. 2. Influence of acclimatisation temperature on the relationship between oxygen consumption ($\dot{M}_{O_2}$) and swimming speed (U). The solid line represents the best-fitting regression: $\dot{M}_{O_2}$=a+bU^c (Eqn 4). The corresponding values for a, b, c and r^2 are given in Table 2.

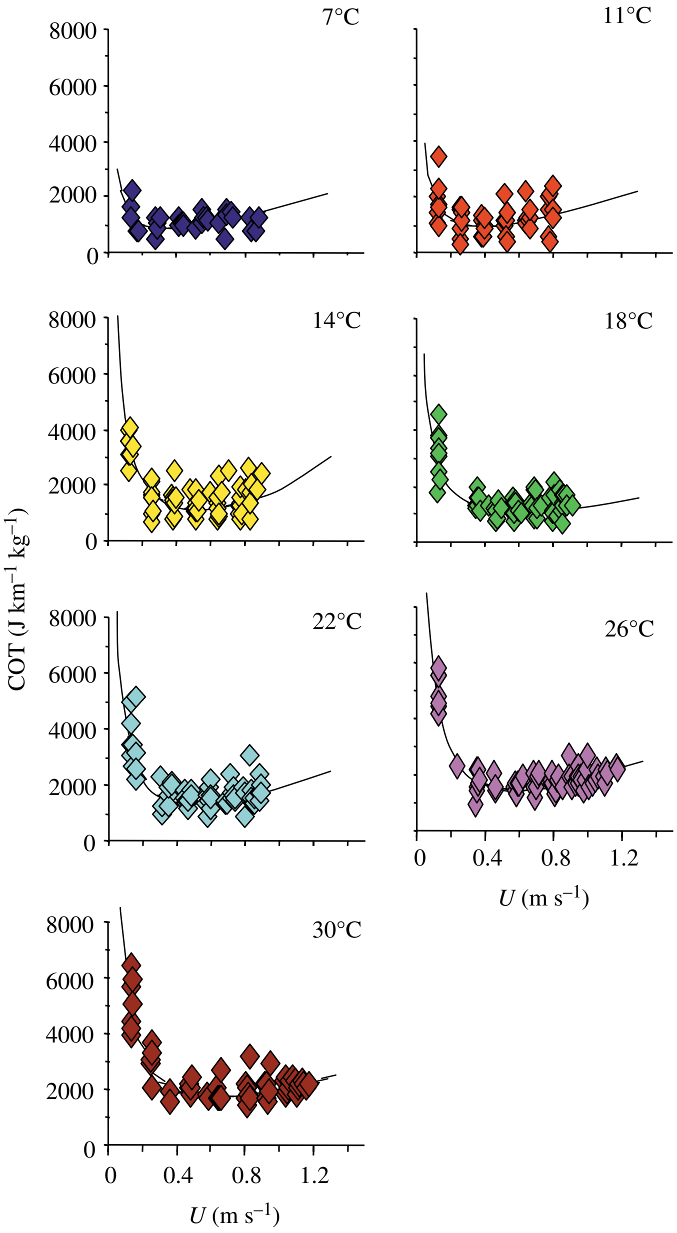

Fig. 3. Relationships between acclimatisation temperature, cost of transport (COT) and swimming speed (U) established using Eqn 6 and the corresponding parameter values from Table 2. The solid lines are a plot of the 3-D model that combines the influence of the temperature and swimming speed on the cost of transport in sea bass, i.e. Eqn 11: COT=5.27[1–exp(–0.007$T^{1.65}$)]/U+(11.44$U^{2.44-1}$).

Eqn 6. We first examined the influence of temperature on the values of the constants a, b and c reported in Table 2. Since b and c followed no clear trend with temperature, average values were calculated (11.44 and 2.44, respectively). The value for parameter a was strongly temperature-dependent. Since a is closely related to standard metabolic rate, the value of parameter a was modelled as a function of temperature by fitting the equation SMR=$f(T)$ proposed for sea bass (Claireaux and Lagardère, 1999). Eqn 4 then became:

$$\dot{M}_{O_2} = 5.27[1-\exp(-0.0077T^{1.65})] + 11.44U^{2.44}\,. \quad (10)$$

The level of fit between observed $\dot{M}_{O_2}$ and modelled $\dot{M}_{O_2}$ was examined using a linear regression (y=0.9307x+24.27; r^2=0.82; F=1709; P<0.0001). From Eqn 10 we derived two equations (see Materials and methods for details). The first one summarises the combined influence of temperature and swimming speed on cost of transport.

$$\mathrm{COT} = 5.27[1-\exp(-0.0077T^{1.65})]\ /\ U + (11.44U^{2.44-1})\,. \quad (11)$$

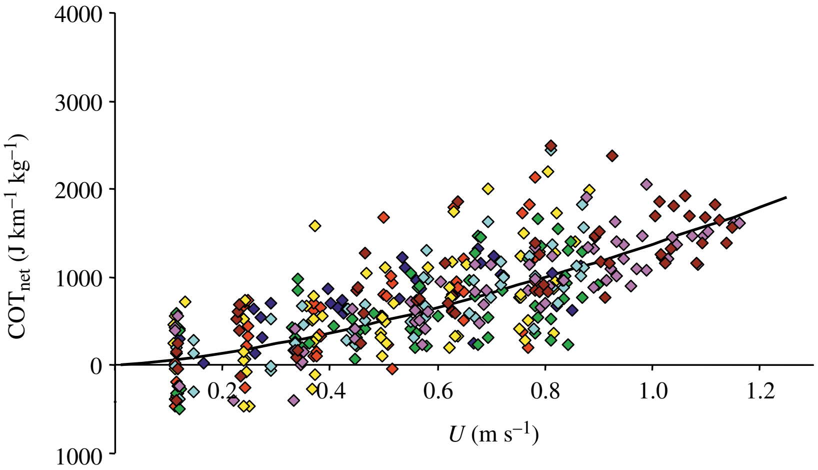

Fig. 4. Relationship between acclimatisation temperature, net cost of transports ($\mathrm{COT}_{\mathrm{net}}$) and swimming speed ($U$). Symbols are calculated $\mathrm{COT}_{\mathrm{net}}$ using Eqn 7. Color-coding matches that in Figs 3 and 4. The solid line is a plot of Eqn 12: $\mathrm{COT}_{\mathrm{net}}=11.44U^{2.44-1}$.

This model corresponds to the solid lines in Fig. 3. The second equation models the influence of swimming speed on the net cost of transport:

$$\mathrm{COT}_{\mathrm{net}} = 11.44U^{2.44-1}\ . \qquad (12)$$

This model is represented as a solid line on Fig. 4.

The various models and experimental data that describe the interactions between temperature, metabolism and swimming performance are summarised in Fig. 5. Open squares are AMR and SMR ± s.e.m. (Table 1). Thick solid lines represent the consolidated models AMR=$f(T)$ and SMR=$f(T)$, which were fitted using the equations reported in Claireaux and Lagardère after combining with the current data set (Claireaux and Lagardère, 1999). Th dotted lines are 'isospeed' curves that were drawn using Eqn 10. Isospeeds depict the influence of water temperature on the cost of swimming at a given speed. The point where one given 'isospeed' meets the AMR=$f(T)$ relationship indicates U_{max} at the considered temperature. Closed triangles are the metabolic rates at U_{opt} for the considered temperature (Table 2).

Discussion

To our knowledge the present study is one of the few that have investigated the effect of thermal acclimatisation upon metabolism and swimming performance in fish (e.g. Butler et al., 1992; Taylor et al., 1996; Day and Butler, 2005). While investigating the influence of seasonal changes in water temperature we specifically examined the link between active metabolic rate and maximum swimming speed. We then modelled the controlling effect of temperature on the cost of swimming. Finally, we conducted an integrative interpretation of the relationships between temperature, metabolism and swimming performance in sea bass.

There are few published measurements of metabolic rate in European sea bass. Oxygen consumption at increasing swimming speed was measured in 250 g, 20°C-acclimated individuals (Herskin and Steffensen, 1998). The relationship established superimposes nicely onto our own results. For instance at U=0.67 m s^{-1}, Herskin and Steffensen report $\dot{M}_{\mathrm{O_2}}$=7.88 mmol h^{-1} kg^{-1}. After correcting for the difference in body mass, Eqn 10 predicts $\dot{M}_{\mathrm{O_2}}$=7.59 mmol h^{-1} kg^{-1}. Claireaux and Lagardère modelled the effect of ambient temperature on bass' active and standard metabolic rates (Claireaux and Lagardère, 1999). We compared both data sets and found a close match between SMR values (Fig. 5). Values for AMR were also very similar, although Claireaux and Lagardère's model tended to underestimate AMR at both ends of the thermal range tested. Apart from differences in the experimental approach we have no satisfying explanation for this discrepancy. We can only emphasise the fact that in the earlier study, fish were larger (500–600 g) and that only four temperatures were tested (10, 15, 20 and 25°C), in contrast to the seven temperatures in the present study. Nevertheless, both data sets were combined, and equation 2 [AMR=$f(T)$] and equation 4 [SMR=$f(T)$] from Claireaux and Lagardère (Claireaux and Lagardère, 1999) were fitted to the consolidated series (thick solid lines in Fig. 5).

Because we were interested in linking aerobic swimming and

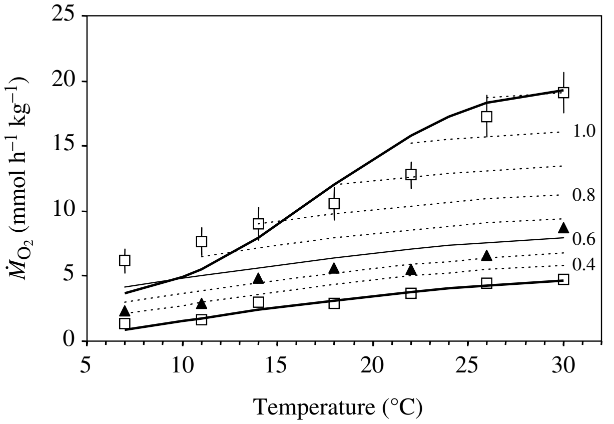

Fig. 5. Summary of the interactions between temperature, metabolism and swimming performance. Open symbols are AMR and SMR ±95% confidence interval (Table 1). Solid bold lines represent consolidated models AMR=$f(T)$ and SMR=$f(T)$, which were fitted using the equations reported in Claireaux and Lagardère (Claireaux and Lagardère, 1999) and after combining the two data sets. Upper line: AMR=$0.00013T^{(-0.033T+4.42)}$+3.25; lower line: SMR=$5.27[1-\exp(-0.0077T^{1.65})]$. The dotted lines are 'isospeed' curves plotted using Eqn 10. The point where one given 'isospeed' curve meets the AMR *versus* T relationship is an indicator of U_{max} at the considered temperature (see Table 1). Closed symbols are $\dot{M}_{\mathrm{O_2}}$ at U_{opt} for the considered temperature (Table 2).

metabolic performances, we chose to examine the maximum swimming speed (U_{max}; see Materials and methods) rather than the critical swimming speed (U_{crit}). U_{crit} is generally defined as the speed at which fish are unable to remove themselves from the posterior grid of the swim chamber (Brett, 1964). Consequently, values for swimming performance reported in Table 1 are slightly lower than the critical swimming speeds found using a true U_{crit} protocol (Chatelier et al., 2005). Nevertheless they are within the range of values reported for most active teleosts (Beamish, 1978; Videler, 1993).

It has long been recognised that the swimming performance of fish is influenced by water temperature (Beamish, 1978). In many fish species, maximum swimming speed or endurance are reduced at low temperature, increase to a peak at an optimum temperature and then decrease as temperature approaches the upper thermal limit (Randall and Brauner, 1991; Myrick and Cech, 2000; Ojanguren and Braña, 2000; Lee et al., 2003). This bell-shaped curve outlines the integrated temperature optima for physiological processes related to swimming and it also prevails in sea bass. Fig. 5 shows that at temperatures above 22–24°C the increase in U_{max} with temperature tends to level off, suggesting that the optimal temperature for sea bass is being attained. Reasons for the drop-off as temperature departs from optimal are many and are not fully elucidated. There is good evidence to suggest that fish reach their maximum aerobic capacities (AMR) at swimming speeds near U_{crit}. This implies that as fish approach maximal swimming, arterial blood is being pumped at the maximum rate by the heart (Farrell, 2002), that arterial blood is fully saturated with oxygen at the gills (Randall and Daxboeck, 1982; Thorarensen et al., 1993; Gallaugher et al., 2001) and that venous blood is maximally depleted of oxygen by the tissues (Farrell and Clutterham, 2003). The present investigation does not provide direct evidence to validate this view but the strong relationship that we found between AMR and U_{crit} as acclimatisation temperature increased (Fig. 1) suggests that the temperature-related changes in cardioresrespiratory performance support the seasonal changes in maximum swimming performance. Along the same lines, aerobic metabolic scope and swimming performance in rainbow trout were positively related to *in vivo* (forced swimming test) or *in vitro* (*in situ* perfused heart preparations) measurements of maximum cardiac pumping capacity (Claireaux et al., 2005). Conversely, oxygen supply to the red muscle was not a limiting factor at exhaustion in trout (McKenzie et al., 2004) and U_{crit} in chinook salmon is virtually independent of functional haemoglobin concentration until [Hb] is less than 50% of control level (Brauner et al., 1993). Moreover, Day and Butler convincingly demonstrated that brown trout acclimated to reversed seasonal temperature displayed reduced swimming ability (U_{crit}) (Day and Butler, 2005), suggesting that more factors than just temperature determined the ability of fish to swim maximally.

It has been shown that temperature has a significant effect on the maximum velocity of shortening of muscle as well as on the maximum power production, while having relatively little effect on sarcomere length excursions and tail beat frequency (Rome, 1990; Rome et al., 1992). On that basis, questions have been raised concerning the mechanisms that allow fish to produce the same movement at different temperatures despite the marked susceptibility of muscle power-generating capacity to thermal conditions. Electromyography studies have shown that during a standardised swim test, only red muscle is recruited at low speed and that anaerobically fuelled, white muscle fibers are recruited at high speed. These experiments also revealed that the recruitment order of the different fibers does not change with temperature but that white muscle fibers are recruited at much lower speed in cold water (Rome et al., 1984). Consequently, it is the compression of the speed range over which motor units are recruited, and the early recruitment of anaerobic fibers, that are believed to explain the reduction in maximal sustainable swimming speed in cold conditions. Our own experimental results clearly support this view. For instance Fig. 4 shows that while maximum swimming speed increases with acclimatisation temperature, the cost of swimming at a given submaximal swimming speed does not change. The lack of thermal effect on $\mathrm{COT}_{\mathrm{net}}$, together with the relatively tight relationship between AMR and U_{max} discussed above, suggest that changes in swimming capacity largely result from variations in energy fluxes and support metabolism, hence in scope for activity, rather than in properties of muscle function *per se* (Rome, 1990; Taylor et al., 1996). However, there are some examples in the literature where swimming cost was shown to be influenced by water temperature (reviewed by Johnston and Temple, 2002). For instance, the energetic costs of swimming at a given speed increased with temperature in the chub mackerel (*Scomber japonicus*) (Dickson et al., 2002). Many reasons can be put forward to explain these inter-species differences, among which species-specific temperature acclimation responses or diversity in molecular mechanisms (Johnston and Temple, 2002). These aspects have not been properly addressed in the literature but their elucidation is a promising avenue for future research.

The current work provides an integrated view of the influence of water temperature on sea bass aerobic swimming performance. However, to convincingly transfer this knowledge into an ecological context, three issues require further investigation. The first concerns the relationship between optimal and spontaneous swimming speeds. Throughout the literature the use of U_{opt} during routine swimming by wild fish is often assumed but this has not been satisfactorily demonstrated, essentially due to technical limitations (Webber et al., 2001a; Webber et al., 2001b). This missing piece of information remains an obstacle to establishing a reliable field energy budget in fish.

The second issue relates to the fact that although the study of locomotion in fish has a long history, little effort has been allocated into investigating the ecological relevance of inter-individual diversity in swimming performance (Kolok, 1999; Plaut, 2001; Nelson and Claireaux, 2005). The basic patterns revealed by Fig. 5 are based on an ‘average fish’ and therefore do not consider inter-individual variability nor phenotypic plasticity. Identifying the potential sources and determinants of such variation is beyond the scope of this paper, but it clearly is the next step in linking locomotor performance to distribution, abundance or fitness of sea bass. In this regard, dietary studies have shown interesting features, including the influence of tissue fatty acid profile on a number of performance traits including cardiorespiratory and swimming performance (McKenzie et al., 1998; McKenzie et al., 2000; McKenzie, 2001; Chatelier et al., 2006).

Finally, swim tests and particularly U_{crit} tests have been used to investigate the relationships between swimming speed and cardiorespiratory variables such as oxygen demand, cardiac and respiratory frequencies, blood gas tensions and cardiac output. However, various authors have questioned the adequacy of a swim-tunnel tests in replicating natural swimming conditions and their energetic implications (Tang and Boisclair, 1995; Plaut, 2001; Nelson et al., 2002). In this regard, Peake and Farrell recently obtained clear evidence for the interference imposed by the size of swim tunnel devices on gait transition (Peake and Farrell, 2004). Energetically speaking, the consequences of this interference remain to be established, but linking the ecological function of swimming and its measure in the laboratory certainly requires that this question be resolved (Swanson et al., 1998; Irschick and Garland, 2001).

List of symbols

AMR	active metabolic rate
A_o	cross-sectional area of the fish
A_t	cross-sectional area of the swim chamber
COT	cost of transport
E	energy expenditure
M_b	body mass
$\dot{M}_{O_2}$	oxygen consumption
MS	metabolic scope
Slope	decrease in water oxygen content per unit time
SMR	standard metabolic rate
U_{max}	maximum swimming speed
U_{opt}	optimal swimming speed
V_F	effective water velocity
VOL_{resp}	volume of the respirometer minus the volume of the fish
V_T	average water velocity
ϵ_s	fractional error in V_T due to blockage
λ	shape factor for the fish [0.53(length/thickness)]
τ	dimensionless factor depending on the tunnel cross-sectional shape

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References

Arnold, S. J. (1983). Morphology, performance and fitness. *Am. Zool.* **23**, 347-361.

Baker, R. R. (1978). *The Evolutionary Ecology of Animal Migration*. New York: Holmes and Meyer.

Beamish, F. W. H. (1978). Swimming capacity. In *Fish Physiology*. Vol. VII (ed. W. S. Hoar and D. J. Randall), pp. 101-187. New York: Academic Press.

Bell, W. H. and Terhune, L. D. B. (1970). Water tunnel design for fisheries research. *Fish. Res. Board Can. Tech. Rep.* **195**, 1-69.

Brauner, C. J., Val, A. L. and Randall, D. J. (1993). The effect of graded methaemoglobin levels on the swimming performance of the chinook salmon (*Oncorhynchus tshawytscha*). *J. Exp. Biol.* **185**, 121-135.

Brett, J. R. (1964). The respiratory metabolism and swimming performance of young sockeye salmon. *J. Fish. Res. Board Can.* **21**, 1183-1226.

Butler, P. J., Day, N. and Namba, K. (1992). Interactive effects of seasonal temperature and low pH on resting oxygen uptake and swimming performance of adult brown trout *Salmo trutta*. *J. Exp. Biol.* **165**, 195-212.

Chatelier, A., McKenzie, D. J. and Claireaux, G. (2005). Effects of changes in water salinity upon exercise and cardiac performance in the European seabass (*Dicentrarchus labrax*). *Mar. Biol.* **147**, 855-862.

Chatelier, A., McKenzie, D. J., Prinet, A., Galois, R., Robin, J., Zambonino, J. and Claireaux, G. (2006). Associations between tissue, fatty acid composition and physiological traits of performance in the sea bass (*Dicentrarchus labrax*). *J. Exp. Biol.* **209**, 3429-3439.

Claireaux, G. and Lagardère, J.-P. (1999). Influence of temperature, oxygen and salinity on the metabolism of European sea bass. *J. Sea Res.* **42**, 157-168.

Claireaux, G., McKenzie, D. J., Genge, A. G., Chatelier, A., Aubin, J. and Farrell, A. P. (2005). Linking swimming performance, cardiac pumping ability and cardiac anatomy in rainbow trout. *J. Exp. Biol.* **205**, 1775-1784.

Day, N. and Butler, P. J. (2005). The effects of acclimation to reversed seasonal temperatures on the swimming performance of adult brown trout *Salmo trutta*. *J. Exp. Biol.* **208**, 2683-2692.

Dickson, K. A., Donley, J. M., Sepulveda, C. and Bhoopat, L. (2002). Effects of temperature on sustained swimming performance and swimming kinematics of the chub mackerel (*Scomber japonicus*). *J. Exp. Biol.* **203**, 3103-3116.

Drucker, E. G. (1996). The use of gait transition speed in comparative studies of fish locomotion. *Am. Zool.* **36**, 555-566.

Farrell, A. P. (2002). Cardiorespiratory performance in salmonids during exercise at high temperature: insights into cardiovascular design limitations in fishes. *Comp. Biochem. Physiol.* **132A**, 797-810.

Farrell, A. P. and Clutterham, S. M. (2003). On-line venous oxygen tensions in rainbow trout during graded exercise at two acclimation temperatures. *J. Exp. Biol.* **206**, 487-496.

Gallaugher, P. E., Thorararensen, H., Kiessling, A. and Farrell, A. P. (2001). Effects of high intensity exercise training on cardiovascular function, oxygen uptake, internal oxygen transfer and osmotic balance in chinook salmon (*Oncorhynchus tshawytscha*) during critical speed swimming. *J. Exp. Biol.* **204**, 2861-2872.

Herskin, J. and Steffensen, J. F. (1998). Energy saving in sea bass swimming in school: measurements of tail beat frequency and oxygen consumption at different swimming speed. *J. Fish Biol.* **53**, 366-376.

Irschick, D. J. and Garland, T. (2001). Integrating function and ecology in studies of adaptation: investigations of locomotor capacity as a model system. *Annu. Rev. Ecol. Syst.* **32**, 367-396.

Johnston, I. A. and Ball, D. (1996). Thermal stress and muscle function. In *Global Warming: Implications for Freshwater and Marine Fish (Society for Experimental Biology Seminar Series 61)* (ed. C. M. Wood and D. G. McDonald), pp. 79-104. Cambridge: Cambridge University Press.

Johnston, I. A. and Temple, G. K. (2002). Thermal plasticity of skeletal muscle phenotype in ectothermic vertebrates and its significance for locomotory behaviour. *J. Exp. Biol.* **205**, 2305-2322.

Kieffer, J. D. (2000). Limits to exhaustive exercise in fish. *Comp. Biochem. Physiol.* **126**, 161-179.

Kolok, A. S. (1991). Photoperiod alters the critical swimming speed of juvenile large mouth bass, *Micropterus salmoides*, acclimated to cold water. *Copeia* **1991**, 1085-1090.

Kolok, A. S. (1999). Inter-individual variation in the prolonged locomotor performance of ectothermic vertebrates: a comparison of fish and herpetofaunal methodologies and a brief review of the recent fish literature. *Can. J. Fish. Aquat. Sci.* **56**, 700-710.

Lee, C. G., Farrell, A. P., Lotto, A., MacNutt, M. J., Hich, S. G. and Healey, M. C. (2003). The effect of temperature on swimming performance and oxygen consumption in adult sockeye (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon stocks. *J. Exp. Biol.* **206**, 3239-3251.

McKenzie, D. J. (2001). Effects of dietary fatty acids on the respiratory and cardiovascular physiology of fish. *Comp. Biochem. Physiol.* **128A**, 607-621.

McKenzie, D. J., Higgs, D. A., Dosanjh, B., Deacon, G. and Randall, D. J. (1998). Dietary lipid composition influences swimming performance in Atlantic salmon (*Salmo salar*) in seawater. *Fish Physiol. Biochem.* **19**, 111-122.

McKenzie, D. J., Piraccini, G., Piccolella, M., Steffensen, J. F., Bolis, C. L. and Taylor, E. W. (2000). Effects of dietary fatty acid composition on metabolic rate and responses to hypoxia in the European eel, *Anguilla anguilla*. *Fish Physiol. Biochem.* **22**, 281-296.

McKenzie, D. J., Wong, S., Randall, D. J., Egginton, S., Taylor, E. W. and Farrell, A. P. (2004). The effects of sustained exercise and hypoxia upon oxygen tensions in the red muscle of rainbow trout. *J. Exp. Biol.* **207**, 3629-3637.

Myrick, C. A. and Cech, J. J. (2000). Swimming performance of four California stream fishes: temperature effects. *Environ. Biol. Fish.* **58**, 289-295.

Nelson, J. A. (1989). Critical swimming speeds of yellow perch *Perca flavescens*: comparison of populations from a naturally acidic lake and a circumneutral lake in acid and neutral water. *J. Exp. Biol.* **145**, 239-254.

Nelson, J. A. and Claireaux, G. (2005). Sprint swimming performance of juvenile European sea bass. *Trans. Am. Fish. Soc.* **134**, 1274-1284.

Nelson, J. A., Gotwalt, P. A., Reidy, S. P. and Webber, D. M. (2002). Beyong U_{crit}: matching swimming performance tests to the physiological ecology of the animal, including a new 'drag strip'. *Comp. Biochem. Physiol.* **133**, 289-302.

O'Brien, C. M., Fox, C. J., Planque, B. and Casey, J. (2000). Climate variability and North Sea cod. *Nature* **404**, 142.

Ojanguren, A. F. and Braña, F. (2000). Thermal dependence of swimming endurance in juvenile brown trout. *J. Fish Biol.* **56**, 1342-1347.

Peake, S. J. and Farrell, A. P. (2004). Locomotory behaviour and post-exercise physiology in relation to swimming speed, gait transition and metabolism in free-swimming smallmouth bass (*Micropterus dolomieu*). *J. Exp. Biol.* **207**, 1563-1575.

Pickett, G. D. and Pawson, M. G. (1994). *Sea Bass: Biology, Exploitation and Conservation (Fish and Fisheries Series 12)*. London: Chapman & Hall.

Plaut, I. (2001). Critical swimming speed: its ecological relevance. *Comp. Biochem. Physiol.* **131**, 41-50.

Quéro, J.-C. (1998). Changes in the Euro-Atlantic fish species composition resulting from fishing and ocean warming. *Ital. J. Zool.* **65**, 493-499.

Quéro, J.-C., Du Buit, M.-H. and Vayne, J.-J. (1998). Les observations de poissons tropicaux et le réchauffement des eaux dans l'Atlantique européen. *Oceanol. Acta* **21**, 345-351.

Randall, D. J. and Brauner, C. J. (1991). Effects of environmental factors on exercise in fish. *J. Exp. Biol.* **160**, 113-126.

Randall, D. J. and Daxboeck, C. (1982). Cardiovascular changes in the rainbow trout (*Salmo gairdneri*) during exercise. *Can. J. Zool.* **60**, 1135-1140.

Rome, L. C. (1990). Influence of temperature on muscle recruitment and muscle function in vivo. *Am. J. Physiol.* **28**, R210-R222.

Rome, L. C., Loughna, P. T. and Goldspink, G. (1984). Muscle fibre activity in carp as a function of swimming speed and muscle temperature. *Am. J. Physiol.* **247**, 272-279.

Rome, L. C., Sosnicki, A. A. and Choi, I. (1992). The influence of temperature on muscle function in the fast swimming scup. I. Shortening velocity and muscle recruitment during swimming. *J. Exp. Biol.* **163**, 259-279.

Sepulveda, C. and Dickson, K. A. (2000). Maximum sustainable swimming speeds and cost of swimming in juvenile kawakawa tuna (*Euthynnus affinis*) and chub mackerel (*Scomber japonicus*). *J. Exp. Biol.* **203**, 3089-3101.

Sokal, R. R. and Rohlf, F. J. (1981). *Biometry*. San Fransisco: W. H. Freeman.

Stebbing, A. R. D., Turk, S. M. T., Wheeler, A. and Clarke, K. R. (2002). Immigration of southern fish species to the south-west England linked to warming of the North Atlantic (1960-2001). *J. Mar. Biolog. Assoc. U. K.* **82**, 177-180.

Swanson, C., Young, P. S. and Cech, J. J., Jr (1998). Swimming performance of Delta smelt: Maximum performance, and behavioral and kinematic limitations on swimming at submaximal velocities. *J. Exp. Biol.* **201**, 333-345.

Tang, M. and Boisclair, D. (1995). Relationship between respiration rate of juvenile brook trout (*Salvelinus fontinalis*), water temperature, and swimming characteristics. *Can. J. Fish. Aquat. Sci.* **52**, 2138-2145.

Tang, Y., Nelson, J. A., Reidy, S. P., Kerr, S. R. and Boutilier, R. G. (1994). A reappraisal of activity metabolism in Atlantic cod (*Gadus morhua*). *J. Fish Biol.* **44**, 1-10.

Taylor, E. W., Egginton, S., Taylor, S. E. and Butler, P. J. (1997). Factors which may limit swimming performance at different temperature. In *Global Warming: Implications for Freshwater and Marine Fish (Society for Experimental Biology Seminar Series 61)* (ed. C. M. Wood and D. G. McDonald), pp. 105-133. Cambridge: Cambridge University Press.

Taylor, S. E., Egginton, S. and Taylor, E. W. (1996). Seasonal temperature acclimatisation of rainbow trout: cardiovascular and morphometric influences on maximal sustainable exercise level. *J. Exp. Biol.* **199**, 835-845.

Thorarensen, H., Gallaugher, P., Kiessling, A. and Farrell, A. P. (1993). Intestinal blood flow in swimming chinook salmon, *Oncorhynchus kisutch*: the effects of hematocrit on blood flow distribution. *J. Exp. Biol.* **179**, 115-129.

Videler, J. J. (1993). *Fish Swimming*. London: Chapman & Hall.

Webber, D. M., Boutilier, R. G., Kerr, S. R. and Smale, M. J. (2001a). Caudal differential pressure as a predictor of swimming speed of cod (*Gadus morhua*). *J. Exp. Biol.* **204**, 3561-3570.

Webber, D. M., McKinnon, G. P. and Claireaux, G. (2001b). Evaluating differential pressure in the European sea bass *Dicentrarchus labrax* as a telemetered index of swimming speed. In *Electronic Tagging and Tracking in Marine Fisheries* (ed. J. R. Sibert and J. Nielsen), pp. 297-314. The Netherlands: Kluwer Academic.