

Scaling of metabolic rate with body mass and temperature in teleost fish

ANDREW CLARKE and NADINE M. JOHNSTON

British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 0ET, UK

Summary

1. We examined published studies relating resting oxygen consumption to body mass and temperature in post-larval teleost fish. The resulting database comprised 138 studies of 69 species (representing 28 families and 12 orders) living over a temperature range of *c.* 40 °C.

2. Resting metabolic rate (R_b ; mmol oxygen gas h^{-1}) was related to body mass (M ; wet mass, g) by $R_b = aM^b$, where a is a constant and b the scaling exponent. The model was fitted by least squares linear regression after logarithmic transformation of both variables. The mean value of scaling exponent, b , for the 69 individual species was 0.79 (SE 0.11). The general equation for all teleost fish was $\ln R_b = 0.80(\ln M) - 5.43$.

3. The relationship between resting oxygen consumption and environmental temperature for a 50-g fish was curvilinear. A typical tropical fish at 30°C requires approximately six times as much oxygen for resting metabolism as does a polar fish at 0°C. This relationship could be fitted by several statistical models, of which the Arrhenius model is probably the most appropriate. The Arrhenius model for the resting metabolism of 69 species of teleost fish, corrected to a standard body mass of 50 g, was $\ln R_b = 15.7 - 5.02.T^{-1}$, where T is absolute temperature ($10^3 \times \text{K}$).

4. The Arrhenius model fitted to all 69 species exhibited a lower thermal sensitivity of resting metabolism (mean $Q_{10} = 1.83$ over the range 0–30°C) than typical within-species acclimation studies (median $Q_{10} = 2.40$, $n = 14$). This suggests that evolutionary adaptation has reduced the overall thermal sensitivity of resting metabolism across species. Analysis of covariance indicated that the relationships between resting metabolic rate and temperature for various taxa (orders) showed similar slopes but significantly different mean rates.

5. Analysis of the data for perciform fish provided no support for metabolic cold adaptation (the hypothesis that polar fish show a resting metabolic rate higher than predicted from the overall rate/temperature relationship established for temperate and tropical species).

6. Taxonomic variation in mean resting metabolic rate showed no relationship to phylogeny, although the robustness of this conclusion is constrained by our limited knowledge of fish evolutionary history.

Key-words: body mass, fish, metabolic cold adaptation, respiration, scaling, temperature.

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Introduction

Faced with the complexity of nature, ecologists have long sought broad patterns as a means of drawing

order from variety. One of the most powerful descriptions has proved to be the striking manner in which many aspects of physiology and ecology scale with body size, and a huge body of information has been accumulated on this topic. Most of these data have, however, been concerned with the terrestrial environment. Despite their being by far the most species-rich chordate group (Nelson 1994), relatively little is known of scaling in fish and in his review of

Correspondence: A. Clarke, Marine Life Sciences Division, British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 0ET, UK. Tel: 01223 221591; Fax 01223 221259; e-mail: andrew.clarke@bas.ac.uk

scaling relationships in nature, Schmidt-Nielsen (1984, p. 72) bemoaned the lack of any general relationship between metabolic rate and body size in fish. Neither of the detailed compilations by Peters (1983) and Calder (1984) were able to provide any general scaling relationships for metabolic rate in fish.

The metabolic rate of all ectothermic organisms is strongly dependent on temperature, as well as body size. This relationship tends, however, to be clearer in aquatic organisms, where the large thermal mass of water buffers the rate of change of environmental temperature experienced by organisms. The evolutionary signal is thus easier to detect against the noise induced by rapid environmental thermal variability. Although relationships between metabolic rate and environmental temperature have long been established for aquatic (primarily marine) invertebrates (for example, Ivleva 1977, 1980; Ikeda 1985), there have been few summary relationships provided for fish. Even recent text-books and reviews of teleost physiology have based their discussion of metabolic rate and temperature largely on the general picture established over three decades ago by Scholander and colleagues (Scholander *et al.* 1953).

The relationship between metabolic rate and temperature in teleosts is of particular interest in relation to the polar environment. A now classic experiment by Ege & Krogh (1914) led to the suggestion that the resting metabolic rates of polar fish would be elevated relative to the rates predicted by the extrapolation to polar temperatures of the resting metabolic rate of temperate water species (Krogh 1914, 1916). This concept of *metabolic cold adaptation* was enormously influential and, although criticized on both experimental (Holeton 1973, 1974) and theoretical grounds (Clarke 1980, 1983, 1991), it has yet to disappear from the literature.

There have, however, been almost no comparative studies of fish metabolism across the ecological temperature spectrum (polar to tropical) since the pioneering work of Scholander *et al.* (1953). A recent exception was a detailed comparative study of the metabolic rate of six species of sedentary marine fish from tropical, temperate and polar habitats, which demonstrated a curvilinear relationship between resting metabolic rate and temperature (Johnston, Clarke & Ward 1991a). This relationship was similar to that previously found for marine invertebrates and it provided no support for the concept of metabolic cold adaptation.

As an adjunct to this detailed comparative experimental study we have undertaken an analysis of literature data on respiration rate in teleost fish. The aims of this study were to:

1. Derive an overall scaling relationship between metabolic rate and body mass in teleost fish, and to

determine any taxonomic variability in this relationship.

2. Derive an overall relationship between resting metabolic rate and temperature for teleost fish, and to determine any taxonomic variability in this relationship.

3. Determine whether this relationship revealed any evidence for metabolic cold adaptation (*sensu* Krogh).

Materials and methods

DATA COMPILATION

There are a great many reports of teleost metabolic rate in the scientific literature, but not all were suitable for inclusion in this study. To obtain a master list of studies we used a combination of published reviews and searches of electronic databases. The original publication for each study was then examined and accepted for our analysis only if it matched all of a number of criteria.

1. All fish were post-larval.
2. The experimental protocol was unlikely to have influenced the measured respiration rate (for example, a sufficient period was allowed for the fish to acclimatize to the experimental chamber).
3. All experimental fish were unfed or post-absorptive, to avoid the effects of feeding on metabolic rate (Jobling 1981).
4. Measurements were of resting metabolism. Often referred to as standard metabolism, this is the respiration rate of an unfed fish resting quietly in the experimental chamber and may be taken as the best experimental approximation to true basal or maintenance metabolic rate (Clarke 1991, 1993).
5. Experimental temperature reflected that experienced by the fish in its natural habitat, was well controlled and reported.
6. Measurements were made over a sufficient range of body mass to allow a precise estimation of the scaling parameters within that species.

These criteria meant that only a small subset of published studies were included in our analysis. These studies were compiled into three separate databases. The largest data set (FULL) comprised 138 studies covering 12 orders, 28 families and 69 species living over a temperature range of $\approx 40^\circ\text{C}$. Many species were, however, represented by studies at more than one temperature and sometimes by more than one study at that temperature. This leads to statistical problems in that species represented by more than one study are unduly weighted in the analysis and can thereby bias the overall relationship. A smaller data set (ONESTUDY) was therefore constructed with each species represented by a single study. The criteria for selection were, first, an experimental temperature most representative of that experienced in the wild, and secondly, the

widest range of body size or the largest number of individuals.

The third database (POLAR) included all studies of polar fish, including those which did not satisfy the criteria for a range of body sizes. This database thus included some studies excluded from the FULL and ONESTUDY databases, but was used only for an examination of specific questions concerned with metabolic cold adaptation.

STATISTICAL ANALYSIS

All literature data for metabolic rate were expressed in terms of oxygen uptake, but this was reported in a wide range of units and often expressed in mass-specific terms. For this analysis all oxygen data were converted to absolute (per individual) rates and molar units (mmol oxygen gas h^{-1}). Conversions from volumetric units were made on the assumption of STP (1 mol oxygen gas occupies 22.4 L). For incorporation into energy budgets metabolic rates should strictly be expressed in units of power. A general conversion may be made on the basis of a mean oxy-calorific coefficient (1 mmol oxygen gas equates to the utilization of 434 J), but this involves an assumption of the substrates being oxidized. Furthermore, most metabolic scaling data are reported in units of oxygen, for this is how they are measured. For these reasons we have not converted literature oxygen utilization data to estimated power consumption.

The scaling equation relating resting oxygen consumption (R_b , mmol h^{-1}) to wet body mass (M , g) is

$$R_b = aM^b$$

where a is a constant and b the scaling exponent (Peters 1983; Calder 1984; Schmidt-Nielsen 1984). The scaling exponent was estimated by the slope of a least squares linear regression following logarithmic transformation of both variables.

The Arrhenius relationship used to model the relationship between absolute temperature, T , and is:

$$R_b = A \exp(-\mu/RT)$$

where A is a constant, μ the Arrhenius constant and R the universal gas constant. Thus, a plot of $\ln R_b$ against T^{-1} yields a straight line of slope $-\mu/R$. An alternative measure of temperature sensitivity is Q_{10} . In this study, Q_{10} was estimated over the range 0–30°C. The fitted Arrhenius model was used to estimate the resting metabolic rate of a 50-g fish at 0°C [$R_{b(0)}$] and 30°C [$R_{b(30)}$]. Q_{10} was then calculated from

$$[R_{b(30)}/R_{b(0)}]^{10/30}$$

A system exhibiting Arrhenius behaviour has a Q_{10} which varies with temperature, but the effect of

this non-linearity of Q_{10} is small over the normal physiological temperature range (see discussion in Clarke 1983).

All statistical analyses were carried out using the standard PC-based packages MINITAB (version 10.1; Minitab Inc, Pennsylvania) and GENSTAT 5 (Payne *et al.* 1993). Where logarithmic transformations were applied, natural (Naperian) logarithms were used, with relevant corrections where original studies used \log_{10} transformation. It is frequently commented that in studies of scaling, least-squares (model I), regression is inappropriate and some form of model II regression is needed (see, for example, Ricker 1973; Laws & Archie 1981); full discussions of this point are those by LaBarbera (1989) and Harvey & Pagel (1991). In the study reported here the independent variables (body mass, temperature) were usually measured with relatively small percentage error and plots of the residuals (not shown here) indicated that the error distributions were independent of body mass or temperature. Model I regression has the benefit of providing residuals that are uncorrelated with the independent variable (in this study, body mass or temperature), whereas model II regression does not (Harvey & Pagel 1991). Model I regression was therefore used in this study.

Results

SCALING OF RESTING METABOLIC RATE WITH BODY MASS

A summary plot of the scaling relationships obtained for individual species (Fig. 1a) suggested that, although species differed markedly in their metabolic rates, this variation was underlain by a general overall scaling relationship between resting metabolic rate and body mass. The frequency histograms of the scaling parameter b for individual studies showed a Gaussian distribution (Fig. 1b), with mean values of 0.791 (SE = 0.011, $n = 138$) for the FULL data set and 0.793 (SE = 0.011, $n = 69$) for the ONESTUDY data set.

Although 110 studies (80% of the FULL data set) reported scaling exponents in the range 0.65–0.95, individual values ranged from 0.40 to 1.29. Analysis of variance indicated a statistically significant variation between different families ($F = 3.50$, $P < 0.001$) and orders ($F = 3.48$, $P < 0.001$). At the level of family these differences were caused mainly by low values of the scaling exponent for Bathydraconidae ($n = 1$) and Gobiidae ($n = 1$), and high values for Myctophidae ($n = 3$) and Ictaluridae ($n = 1$). At the level of order, the differences were caused mainly by high mean values for Myctophiformes ($n = 3$) and Salmoniformes ($n = 13$).

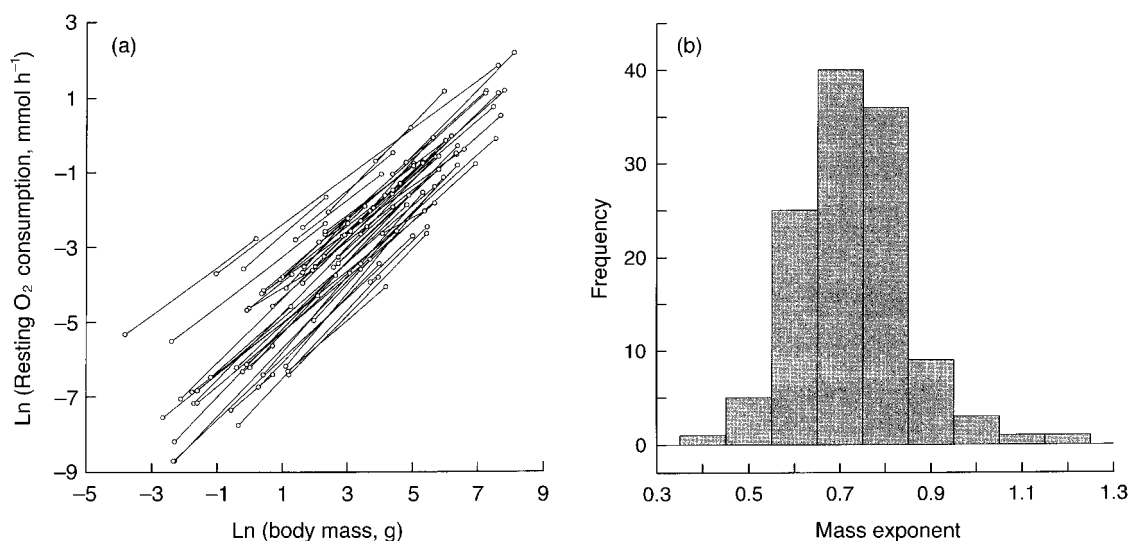


Fig. 1. (a) Relationship between resting oxygen consumption (mmol h⁻¹) and body mass (g) for teleost fish. Each line represents the scaling relationship determined for a particular species, plotted between the maximum and minimum body masses used in that study. Data from ONESTUDY data set, so each species is represented only once. A small number of studies have been omitted for clarity. (b) Frequency histogram of literature values of the within-species scaling exponent, *b*, for teleost fish. FULL data set (*n* = 138 studies, 69 species).

Despite this natural variability, the overall relationships shown in Fig. 1(a) and Fig. 1(b) suggest that a log/log model with a scaling exponent of 0.79 is a suitable statistical model to provide a first-order description of the overall relationship between resting metabolic rate and body mass in teleost fish. Such statistical models, whilst undoubtedly obscuring some important biological variability, are of great heuristic value in drawing broad ecological conclusions. The overall relationship was $\ln R_b = 0.80(\ln M) - 5.43$.

Scaling exponents determined within species may, however, differ from those between species, for both evolutionary and statistical reasons (see discussion by Harvey & Pagel 1991). An estimate of the between-species scaling exponent for teleost fish was derived by calculating the mean resting metabolic rate of a fish of median size for each experimental species and fitting an overall scaling relationship to logarithmically transformed data (Fig. 2). The slope of the model I regression line was 0.801 (SE = 0.062, *n* = 69; data from the ONESTUDY data set). The between species and the mean within-species mass exponents in teleost fish are thus effectively identical.

Although there is clearly a strong scaling relationship between resting metabolic rate and body mass in teleost fish, the data show considerable scatter about the regression line (Fig. 2). An important factor in explaining this remaining variance is environmental temperature.

SCALING OF RESTING METABOLIC RATE WITH TEMPERATURE

Before examining the relationship between resting metabolic rate and temperature it is necessary first to remove the effect of body mass. Two widely used techniques are either to analyse the residuals around

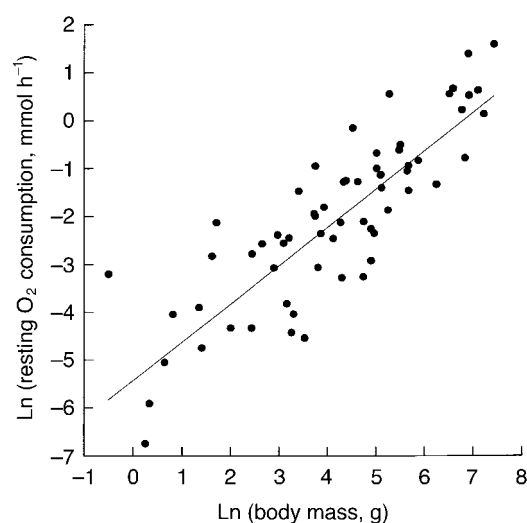


Fig. 2. Between-species scaling relationship between resting oxygen consumption (R_b , mmol h⁻¹) and wet body mass (M , g) in teleost fish. Each species is represented by a single data point (ONESTUDY data set). The overall model I regression is $\ln R_b = 0.80(\ln M) - 5.43$.

the metabolic rate/body mass relationship (Bennett 1987) or to correct data for each species to a given size. These techniques produce similar qualitative results; the data presented here are for metabolic rate corrected to a standard size of 50 g (close to the median size of all fish in the study, which was 47 g). This correction utilized the species-specific mass exponent determined in the original study. The qualitative patterns were the same if the mean between-species exponent was used for all studies.

A linear plot of the data (Fig. 3a) reveals a monotonic curvilinear relationship between metabolic rate and temperature in teleost fish. This is strikingly similar to relationships established previously for aquatic invertebrates (Ivleva 1977, 1980; Ikeda 1985; summarized in Clarke 1991) and it indicates that a typical tropical fish living at 30°C requires consider-

ably more oxygen for resting metabolism than does a polar fish at 0°C.

Ecologists typically prefer to work with linear rather than curvilinear relationships, and there are several transformations that are effective at linearizing the relationship between resting metabolic rate and temperature. These include log/linear (Fig. 3b), log/log (Fig. 3c) and Arrhenius models (Fig. 3d). All of these statistical models predict a similar increase in resting oxygen requirement for tropical fish relative to that of polar fish (range $\times 5.9$ to $\times 6.2$) and all explain similar amounts of the overall variation in resting metabolic rate (55–59%). The remaining variance will include both experimental error, and any effects of phylogeny, ecology or life-style. The latter three influences are, of course, likely to be linked.

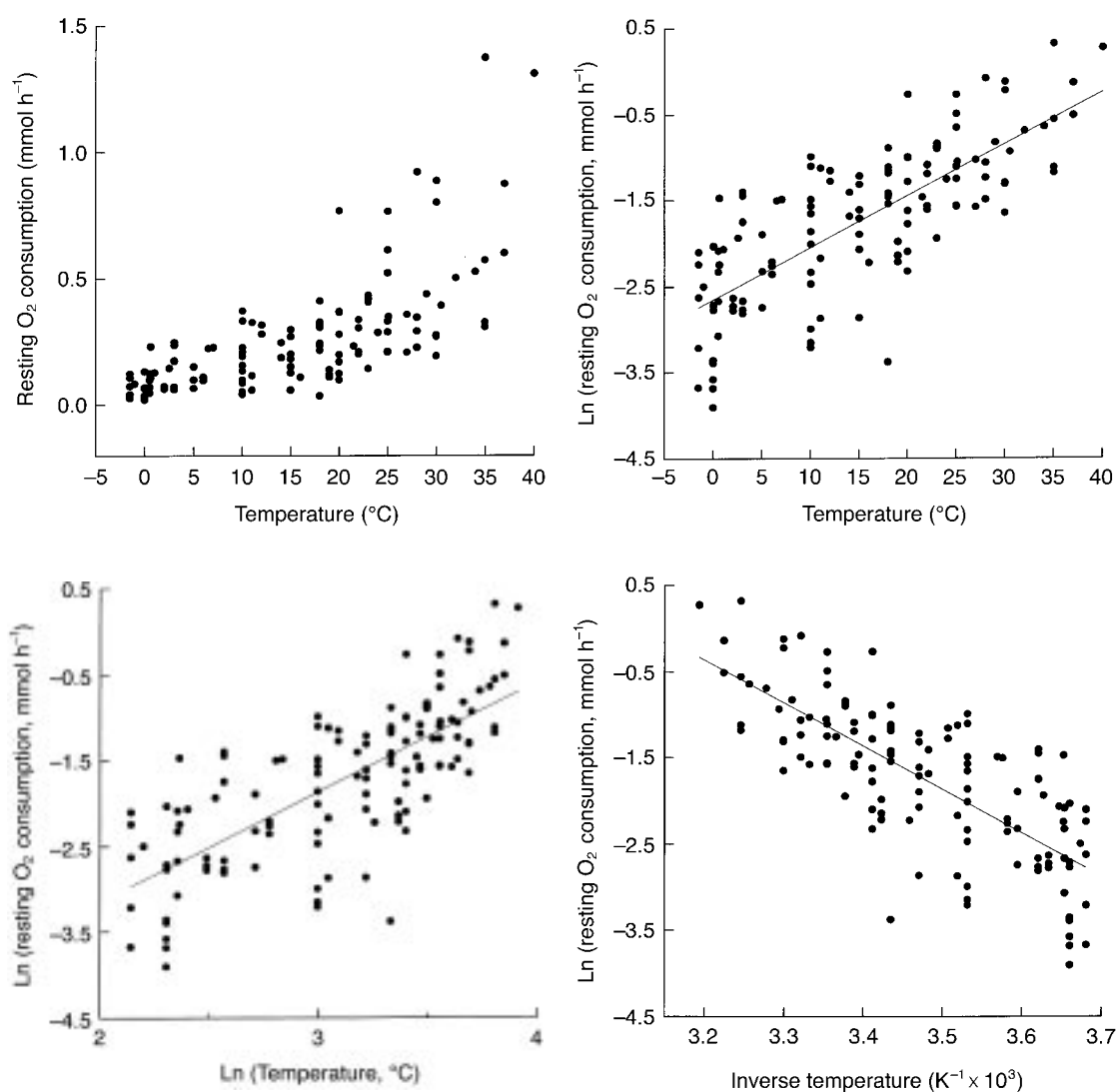


Fig. 3. Relationship between resting oxygen consumption (R_b , $mmol\ h^{-1}$) and temperature for teleost fish, with different fitted statistical models. All data corrected to a size of 50 g wet mass; data shown are from ONESTUDY data set, although the FULL data set gave similar relationships. (a) Linear plot; note elevation of abscissa for clarity. (b) Log/linear plot with fitted least-squares regression line. (c) Log/log plot with fitted least-squares regression line. (d) Arrhenius plot, with fitted least-squares regression line.

The influence of phylogeny on resting metabolic rate was examined for two of the linear statistical models, the double logarithmic (Fig. 3c) and Arrhenius (Fig. 3d). The results were closely similar and only the analysis of the Arrhenius data is discussed here.

TAXONOMIC VARIATION IN RESTING METABOLIC RATE

Analysis of covariance (ANCOVA) was used to examine the relationship between resting metabolic rate and temperature for differing levels of taxonomic aggregation, using data from the ONESTUDY data set. Pooling of data by family provided insufficient data for ANCOVA; too many families were represented by only a single study or the temperature range represented in the data was too low ($< 10^{\circ}\text{C}$). Analysis of data pooled by order did, however, reveal a significant effect.

ANCOVA provided no evidence to reject the null hypothesis that the slope of the relationship between metabolic rate and temperature was the same for each order of teleost fish ($F = 1.74$, $P > 0.10$). There were, however, highly significant differences in elevation ($F = 12.7$, $P < 0.001$) indicating that the resting metabolism of fish from different taxonomic groups varied significantly (Fig. 4). The highest mean rest-

ing metabolic rates were shown by gadoids and the lowest by eels (Table 1).

Although ANCOVA revealed significant differences in mean resting metabolic rate between different taxa of teleost fish, the large variance indicates a high degree of overlap in the data (Fig. 4). The pooled Arrhenius model (Fig. 3d), thus provides a valid first-order statistical model for the overall relationship between resting metabolic rate and temperature in teleost fish. This relationship is $\ln R_b = 15.7 - 5.02 \cdot T^{-1}$.

DO POLAR FISH SHOW METABOLIC COLD ADAPTATION?

The concept of metabolic cold adaptation is that polar fish should show a resting metabolic rate greater than the rate predicted by extrapolation to polar temperatures of the resting metabolic rate of temperate or tropical fish. Although originally proposed by Krogh (1914, 1916), this idea was most convincingly espoused by Scholander *et al.* (1953), Wohlschlag (1960) and Dunbar (1968). So much so that for a long time metabolic cold adaptation was the defining paradigm for investigations of evolutionary adaptation in polar marine organisms (see discussions by Clarke 1980, 1983, 1991).

A number of studies of metabolic cold adaptation have compared the metabolic rate of polar fish with

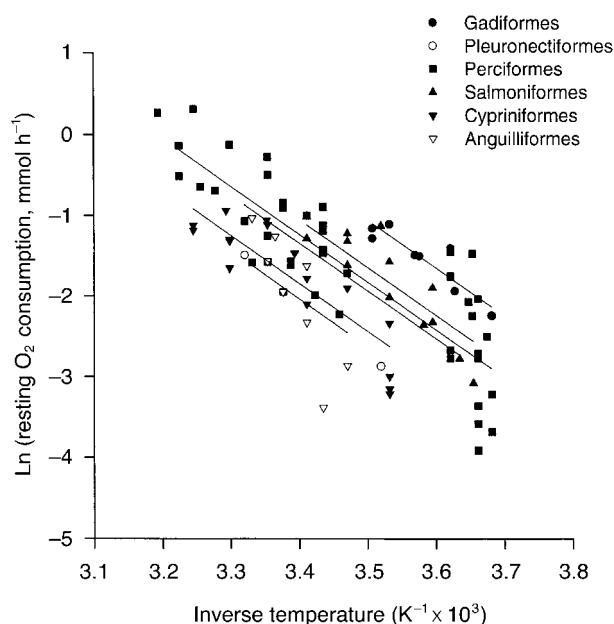


Fig. 4. Analysis of covariance for the relationship between resting metabolic rate and temperature for teleost fish, with data pooled by taxonomic order. Data are from the FULL data set, with fitted Arrhenius statistical models. Symbols represent different orders, with regression lines from ANCOVA shown; in order of decreasing metabolic rate the lines are for Gadiformes (●), Pleuronectiformes (○), Perciformes (■), Salmoniformes (▲), Cypriniformes (▼), and Anguilliformes (▽). Analysis of the ONESTUDY data set revealed a similar pattern, except that two data sets (Anguilliformes, Gadiformes) had to be excluded because of insufficient data. ANCOVA using a double logarithmic statistical model fitted to both the ONESTUDY and FULL data sets gave closely similar results.

Table 1. Taxonomic variation in the relationship between resting oxygen consumption (R_b , mmol h^{-1}) and temperature in teleost fish. Taxonomy follows Nelson (1994). The individual scaling relationships between resting metabolic rate (mmol h^{-1}) and body mass (g) were used to estimate the oxygen consumption of a 50-g fish. These data were then fitted by an Arrhenius model, with regression lines fitted individually to each order by ANCOVA (Fig. 4). These relationships were then used to predict the resting metabolic rate of a 50-g fish at 15°C . The six orders included in the ANCOVA include 55 of the 69 species examined in this study. Note that the standard error (SE) has been back-transformed from natural logarithms

Order	Number of Families	Genera	Species	Predicted metabolic rate Mean	SE
Gadiformes	1	3	4	0.417	0.078
Pleuronectiformes	5	8	8	0.173	0.298
Salmoniformes	2	4	6	0.231	0.033
Perciformes	10	17	30	0.193	0.013
Cypriniformes	2	5	5	0.104	0.013
Anguilliformes	1	1	2	0.086	0.016

that of temperate species (reviewed by Macdonald, Montgomery & Wells 1987). Whilst Johnston *et al.* (1991a) attempted to control for ecology and life-style, no comparative studies to date have controlled for phylogeny. This is potentially a problem because the Southern Ocean fish fauna is most unusual in being dominated ecologically by the radiation of a single perciforme suborder, the notothenioids (Eastman 1993; Clarke & Johnston 1996; Eastman & Clarke 1998). Given the significant variation of mean resting metabolic rate with phylogeny (Fig. 4; Table 1) the only valid test of metabolic cold adaptation is to confine the analysis to perciformes and compare the resting metabolic rates of polar notothenioids with the metabolic rates of non-polar perciforme fish. When this is done there is no evidence that the resting metabolic rates of notothenioids is detectably different from that predicted from the relationship between metabolic rate and temperature of non-polar perciforme fish (Fig. 5).

Perciformes are the most speciose teleost order (Nelson 1994), and comprise fish with a wide range of morphology and ecology. The variance about the regression line (Fig. 5) also indicates that there is a considerable diversity of resting metabolic rate. Zoarcids (eel-pouts) in particular have a somewhat sedentary life-style and a low metabolic rate. Wohlschlag (1963) described the Antarctic *Rhigophila dearborni* as having an unusually low metabolism, but Holeyton (1974) was able to show that this was a feature of zoarcids as a taxon and that a comparative study of zoarcid metabolism afforded no support for metabolic cold adaptation.

The only other teleost order for which there are sufficient polar and non-polar data to test for metabolic cold adaptation is Gadiformes (true cods). These show no evidence for metabolic cold adaptation (data not shown) although the robustness of this conclusion is limited by the few data available (Holeyton 1974).

Discussion

BODY MASS SCALING EXPONENT

The mean within-species (intraspecific) mass scaling exponent for teleost fish was 0.79 (SE 0.11, $n = 138$). Although a scaling exponent of about 0.75 is commonly reported for the between-species relationship between resting or basal metabolic rate, and body mass in ectotherms, there is no generally accepted theoretical explanation for this value. Discussion of this topic started over a century ago

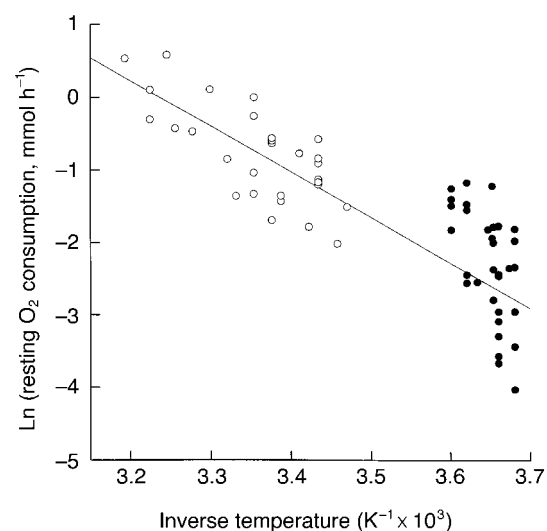


Fig. 5. A test of metabolic cold adaptation. The resting metabolic rate of notothenioid fishes from the Southern Ocean (●) compared with that of other (non-notothenioid) perciforme fish from warmer waters (○). The data are presented as an Arrhenius plot, and the line fitted to all non-polar data. The polar data show no evidence of significant metabolic cold adaptation (*sensu* Krogh: a tendency for polar species to lie above the fitted line). The polar data include several studies not included in either the FULL or ONESTUDY data sets (see methods).

(Rubner 1883) and many of the key arguments were explored by Zeuthen (1947, 1953). Nevertheless, despite attempts based on surface area/volume considerations, the incorporation of physiological time, biological similarity and strict dimensional analysis (see discussions in Peters 1983; Schmidt-Nielsen 1984; and Calder 1984) nobody has been able to derive a convincing or universally accepted prediction of the value of the scaling exponent from first principles. A recent suggestion has been that of Kooijman (1993), who used dynamical energy budget theory to conclude that the exponent is a weighted sum of surface area and volume. Kooijman argued that the actual value thus lies within the bounds 0.66 and 1, depending on the role of energy metabolism in thermoregulation, with predictions of lower values (≈ 0.66) for endotherms, and higher values (closer to 1) for pure ectotherms. Most recently, West, Brown & Enquist (1997) have deduced a value of ≈ 0.75 for inter-specific allometry based on physiological constraints associated with the architecture of branching vascular systems. The difficulty with many of these suggestions is that of deciding which feature of a tightly integrated physiology represent the true evolutionary constraint, and which features are co-adaptations optimized to a constraint elsewhere.

Whereas an intra-specific scaling exponent is useful for studies of within-species energetics, general models applicable to all fish require a between-species (inter-specific) scaling exponent. These two exponents may be different, for both statistical and evolutionary reasons (see discussion by Harvey & Pagel 1991), and Kozłowski & Weiner (1997) have recently suggested that inter-specific scaling reflects the overall pattern of body size optimization at the individual species level. Calder (1984) also cautions against mixing ontogenetic and phylogenetic data in studies of scaling. In the study reported here, the inter-specific scaling exponent was 0.80, which is statistically indistinguishable from the mean within-species value. This mean value is also very similar to that calculated by Schmidt-Nielsen (1984) from a much smaller data set and to the overall mean value calculated for endotherms by Peters (1983), which was 0.74 (SE = 0.11, $n = 146$).

RESPIRATION AND TEMPERATURE

The resting oxygen consumption of teleost fish was found to vary significantly with temperature (Fig. 3). The estimate of the factorial increase in resting metabolism comparing a representative tropical (30°C) and polar (0°C) teleost depended on the statistical model fitted, and ranged from 5.9 (log/log model) to 6.2 (Arrhenius model). This indicates that a typical tropical fish consumes roughly six times as much oxygen as does a typical polar fish and, hence,

must find six times as much food per unit time simply to fuel resting metabolism. The difference will likely be even greater for overall power budgets incorporating the annual costs of locomotor activity and growth, both of which are generally greater in tropical fish (Bennett 1985; Clarke & North 1991; Johnston *et al.* 1991a; Kock & Everson 1998).

Although any one of the four models shown in Fig. 3 would allow the resting metabolism of a fish to be estimated on the basis of its mass and environmental temperature, we disagree with Peters (1991) that these may in any way be construed as theory. The various plots are simply statistical models which summarize observations in a convenient manner. It remains a major difficulty in thermal ecology that we have as yet no theory which can explain or predict from first principles the relationship to be expected between whole organism resting metabolism and environmental temperature in ectotherms (Clarke 1991, 1993).

The Arrhenius relationship provides an excellent description of the relationship between reaction rate and temperature for a simple chemical system. Furthermore, the form of this relationship can be deduced from first principles for it is based firmly on statistical thermodynamics. It might therefore be regarded as a valid model of whole-animal thermal physiology, if it could be assumed that the key physiological processes involved in energy metabolism form an integrated whole that behave in the same way with respect to temperature as do the isolated component systems (a suggestion which originated at least as far back as Krogh 1916). It is not clear to what extent this assumption can be justified, other than by the existence of extensive and subtle controls that regulate whole-animal physiology. On the other hand, the log/log and log/linear (exponential) models are no more than traditional statistical transformations which have proved effective in linearizing many biological relationships. In the absence of any alternative theory or explanation, the Arrhenius relationship is therefore probably the most appropriate statistical description of whole-animal thermal physiology.

The Arrhenius statistical model fitted to the ONESTUDY data set (Fig. 3d) is equivalent to a between-species Q_{10} of 1.83 over the temperature range 0–30°C. (Systems exhibiting Arrhenius behaviour have a Q_{10} , which varies inversely with temperature, although the effect is small over the ecological temperature range: Clarke 1983.) This is smaller than typical within-species acute Q_{10} values reported in the literature. Of the 138 studies examined here, 14 reported Q_{10} values; these ranged from 0.45 to 3.41 with a median of 2.40 (the frequency distribution being negatively skewed). This suggests that evolutionary temperature adaptation has produced a between-species relationship that has a

lower thermal sensitivity than is typical of within-species relationships. Although there remains a significant difference between the rate of resting metabolism in typical polar and tropical teleosts, this is less than would be expected on the basis of the thermal sensitivity of individual species determined in experimental studies.

METABOLIC COLD ADAPTATION

In considering the evolutionary adaptation of teleost fish to environmental temperature, probably the single most contentious aspect has been that of metabolic cold adaptation. The pioneering Danish respiratory physiologist August Krogh undertook a now classic experiment in which a single goldfish, *Carassius auratus*, was exposed to a series of temperatures and its oxygen consumption measured (Ege & Krogh 1914). The experiment produced a roughly exponential decrease in respiration rate as the temperature was lowered, and this relationship became known as Krogh's normal curve.

Krogh (1914, 1916) made the intuitively reasonable prediction that fish which had evolved to live at polar temperatures would be expected to have evolved some form of compensation for the rate-depressing effect of temperature he had observed in his goldfish. Specifically, the prediction was that the metabolic rate of fish that had evolved to live at polar temperatures would be higher than the rates exhibited by temperate fish cooled to polar temperatures (or the rates predicted by extrapolation to polar temperatures of the metabolic rate/temperature relationships established for warmer water fish), the end result of this evolutionary process being termed *metabolic cold adaptation*. Although the concept was established explicitly in terms of respiratory physiology, it was subsequently extended to measures such as the activity of individual metabolic pathways or enzymes.

Early measurements of the metabolic rate of polar fish appeared to confirm Krogh's prediction, thereby establishing the concept of metabolic cold adaptation firmly in the literature of comparative and evolutionary physiology (Scholander *et al.* 1953; Wohlschlag 1960, 1964; and many subsequent textbooks and reviews).

The next development was an exceptionally careful series of measurements by Holeyton (1973, 1974), which showed clearly that there was no convincing experimental evidence for an elevated metabolic rate in polar fish. Holeyton explained the early results which appeared to support the concept of metabolic cold adaptation as being caused partly by genuinely elevated metabolic rates induced by the experimental protocol. Holeyton (1974) was the first to recognize that polar fish need much longer periods of acclimation to experimental apparatus than do temperate

or polar fish, an effect now thoroughly confirmed by both time-course (Morris & North 1984) and hormonal (Egginton 1994) studies. Slow gut-passage times in polar fish also extend the period over which post-prandial increases in metabolic rate are observed (Johnston & Battram 1993; Boyce & Clarke 1997).

Neither the careful experimental work of Holeyton (1973, 1974) nor theoretical arguments (Clarke 1980, 1991, 1993) resulted in the demise of the concept of metabolic cold adaptation. Recent studies have concluded that there may be a small elevation of resting metabolic rate in polar fish (perhaps by a factor of 2: Forster *et al.* 1987; Torres & Somero 1988), but these comparative studies have usually involved only a limited range of species. The detailed examination of the resting metabolic rate of tropical, temperate and polar fish of similar size and life-style (Johnston *et al.* 1991a), and the comparison here for perciform fish (Fig. 4) have, however, confirmed the conclusion first promulgated by Holeyton (1974): metabolic cold adaptation (*sensu* Krogh) does not exist.

THE INFLUENCE OF PHYLOGENY

It is now well recognized that to achieve a true evolutionary perspective in comparative studies it is necessary to control for phylogeny (Harvey & Pagel 1991). Closely-related species are likely to have diverged from a common ancestor only recently and, hence, to have had less time to accumulate differences than more distantly related species. This can lead to a phylogenetically-based pseudo-replication in comparative studies and unless phylogeny is controlled for statistically, results in an increased incidence of Type 1 errors.

In the absence of a detailed phylogeny for the species examined in this study, we have instead undertaken an analysis of covariance. Data were aggregated at the level of order for ANCOVA; when data were aggregated at lower taxonomic levels (family, genus) there were too many missing observations to permit statistical analysis. This analysis revealed statistically significant differences in resting metabolic rate between the six orders for which we had sufficient data (Fig. 4; Table 1). This result is similar to that obtained by Pauly (1980) for the mortality rate of different taxa of fish living at different temperatures.

Although there are significant differences between different teleost orders in mean resting metabolic rate, there is also substantial variation within major taxa. Thus, different species within a given order may vary markedly in metabolic rate, even after controlling for body mass and temperature. This variation is correlated with ecology and, particularly, with broad patterns of activity. Thus, in polar

notothenioids, resting metabolic rate increases from less active to more active species (Morris & North 1984) and this is true of polar fish in general (Zimmerman 1997). It would thus appear that the evolution of particular lifestyles brings with it a concomitant associated metabolic cost, as has been shown in muroid rodents (Koteja & Weiner 1993).

By analogy with data emerging for birds (Daan, Masman & Groenewold 1990), it would seem likely that broad differences in resting metabolic rate of fish are caused by changes in the relative proportions of body organs with differing inherent mass-specific metabolic demands. Because the anatomical configuration of species is likely to be more conserved within lineages than between lineages, this would explain the observed differences in mean resting metabolic rate between major taxa.

It would therefore be instructive to map the observed resting metabolic rates onto a secure phylogeny to undertake a thorough analysis of evolutionary trends. Unfortunately, there is no phylogeny available for the species used in this study and even the topology at the level of order is not well resolved. Nevertheless, it is clear that there is no strong relationship between higher level phylogeny and resting metabolic rate, since the euteleost clade incorporates taxa with the highest and one of the lowest resting metabolic rates (Fig. 6).

Taxonomic (and by inference, phylogenetic) differences in the resting metabolic rate of fishes are probably related to lineage-specific variations in body architecture and, specifically, the relative proportions of the major body organs. Variations in resting metabolic rate within major taxa are asso-

ciated with differences in lifestyle (and particularly in activity) between species, possibly mediated through factors such as differences in mitochondrial density and associated physiological costs. These patterns would suggest that broad differences between major lineages in physiology have no phylogeny-specific component. Phylogenetically-linked differences appear merely as epiphenomena because the proximal causes of differences in physiology, such as differences in anatomical and physiological organization, tend to be more similar within lineages than between lineages.

The ANCOVA also suggests that when comparison is made between different taxonomic orders (for example, gadoids and eels: Fig. 4) there is a tendency for resting metabolic rate at representative environmental temperatures to be more similar than the overall relationship across the species within an order. The degree of temperature sensitivity thus decreases in the sequence species > within orders > between orders.

THE EVOLUTION OF METABOLIC RATE

The correlation of resting metabolic rate with environmental temperature (Fig. 3) and the variation between major taxa (Fig. 4) pose the question of what are the key driving forces behind the evolution of a particular metabolic rate. What dictates that one type of fish has a higher or lower resting metabolic rate than another, and why is resting metabolic rate so much higher for a tropical than a polar fish?

The lower thermal sensitivity of resting metabolic rate between species ($Q_{10} = 1.83$) compared with that observed typically in acclimation studies (med-

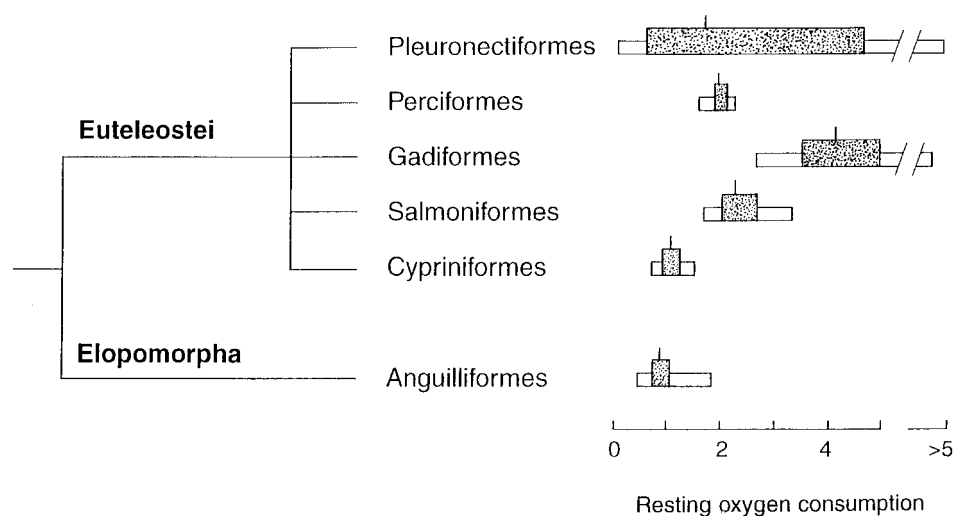


Fig. 6. Estimated resting oxygen consumption of a 50-g fish at 15°C from the different teleost orders examined in this study, superimposed on a working phylogeny. Taxonomy and cladogram topology from Nelson (1994). The metabolic rate data plotted are mean (line), one standard error (stippled bar) and 95% confidence intervals for the mean (open bar), estimated from ANCOVA.

ian $Q_{10} = 2.40$) suggests a degree of evolutionary adjustment. It is not clear whether the lower thermal sensitivity of the evolutionary relationship is the result of a high resting metabolic rate at lower temperatures, a reduced resting metabolic rate at higher temperatures or a combination of both.

A subtle but important distinction which needs to be drawn here is that between an overall evolutionary adjustment to the thermal sensitivity of resting metabolic rate, and metabolic cold adaptation (*sensu* Krogh). The former applies across the complete physiological temperature range (roughly -2°C to $+40^{\circ}\text{C}$ for teleost fish), whereas the latter hypothesis predicted a temperature/resting metabolic rate relationship for polar fish different in kind from all other fish. It is also possible that the between-species relationship (Fig. 3) is simply an epiphenomenon resulting from physiological optimization at the species level and thus requires no evolutionary explanation.

A major problem for thermal physiologists attempting to explain the relationship between temperature and metabolic rate is that it is not at all clear what physiological processes are operating faster in a resting tropical fish (or slower in a resting polar fish). It seems likely that protein turnover, membrane homeostasis and cellular ion balance are all important (Hawkins 1991; Clarke 1993), although neither the relative contribution of each of these to maintenance metabolism, nor how these vary with temperature or lifestyle, are known with any certainty.

Resting metabolism does, however, represent a cost to the organism in that energy utilized in maintenance must be met from food or reserves. It cannot be used in processes that contribute to evolutionary fitness, such as growth, reproduction or behavioural activity (other than in the trivial sense that a dead organism has zero fitness). Thus, although it is easy to recognize in principle the fitness advantage to be gained from an enhanced scope for growth or increased scope for activity, it is much more difficult to discern an evolutionary advantage to an elevated resting or maintenance metabolic rate. This problem was recognized early in the debate over metabolic cold adaptation (Dunbar 1968; Somero, Giese & Wohlschlag 1968), but not resolved.

It has long been known for a variety of taxa that within a species there is often an inverse correlation between resting metabolic rate and growth rate (Hawkins 1991). Such variability within a species provides raw material for evolutionary change, but does not explain why resting metabolic rate varies between taxa as it does. The study reported here shows that there is an energetic advantage to living in cold water in terms of decreased maintenance costs (or alternatively a disadvantage in terms of

increased costs for tropical species). The question is, thus, what evolutionary forces are keeping tropical resting metabolic rates high? At present we do not know, and why the relationship between resting metabolic rate and temperature is what it is remains an intractable problem for physiological ecologists.

One possible factor is the extent to which evolutionary adjustment to temperature allowing a reduced resting metabolic rate has also constrained the capacity to generate metabolic power. If relative aerobic scope (the ratio of peak power to resting power) remains more or less independent of temperature, then absolute metabolic power is greatly reduced in polar species. Thus, for a constant relative aerobic scope of $\times 5$ a representative polar species at 0°C can generate 0.33 W extra power above resting metabolism, whereas a representative tropical species at 30°C could generate an extra 2.05 W (data for a representative 50-g fish, calculated from the overall Arrhenius statistical model: Fig. 3d). This considerable difference may have enormous ecological significance.

It is not yet clear, however, the extent to which relative aerobic scope varies with temperature or the extent to which polar species have a reduced capacity to generate metabolic power, but this is an active area of research (Johnston, Johnson & Battram 1991b; Boyce & Clarke 1997; Johnston *et al.* 1998).

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