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Comparative metabolic rates of common western North Atlantic Ocean sciaenid fishes

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The resting metabolic rates (R_R) of western North Atlantic Ocean sciaenids, such as Atlantic croaker *Micropogonias undulatus*, spot *Leiostomus xanthurus* and kingfishes *Menticirrhus* spp., as well as the active metabolic rates (R_A) of *M. undulatus* and *L. xanthurus* were investigated to facilitate inter and intraspecific comparisons of their energetic ecology. The R_R of *M. undulatus* and *L. xanthurus* were typical for fishes with similar lifestyles. The R_R of *Menticirrhus* spp. were elevated relative to those of *M. undulatus* and *L. xanthurus*, but below those of high-energy-demand species such as tunas *Thunnus* spp. and dolphinfish *Coryphaena hippurus*. Repeated-measures non-linear mixed-effects models were applied to account for within-individual autocorrelation and corrected for non-constant variance typical of noisy R_A data sets. Repeated-measures models incorporating autoregressive first-order [AR(1)] and autoregressive moving average (ARMA) covariances provided significantly superior fits, more precise parameter estimates (*i.e.* reduced S.E.) and y-intercept estimates that more closely approximated measured R_R for *M. undulatus* and *L. xanthurus* than standard least-squares regression procedures.

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Key words: intermittent-flow respirometry; metabolism; mixed-effects models; repeated measures; Sciaenidae.

INTRODUCTION

Energy acquisition and allocation are fundamental processes that integrate organismal physiology, behaviour and biophysics. Ingested energy is apportioned to metabolic requirements and wastes before surpluses can be routed to somatic and gonadal growth (Winberg, 1956; Hewett & Kraft, 1993). Interest in the description, quantification and prediction of energy acquisition and allocation patterns of fishes has led to the development of bioenergetic and individual-based models (Kitchell *et al.*, 1977; Boisclair & Tang, 1993; Jobling, 1994). These models link physiology, behaviour

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and environmental conditions with population dynamics to provide system-level estimates of production and consumption (Kitchell *et al.*, 1977; Brandt & Hartman, 1993). Catabolism, generally the largest and most labile component of the energy budgets of fishes, must particularly be understood for such models to generate valid results (Boisclair & Sirois, 1993; Ney, 1993).

Aerobic metabolism ranges from the standard metabolic rate [R_S , the rate of oxygen consumption (M_{O_2}) of an inactive, unfed, thermally acclimated subject at rest: Krogh, 1914; Brett & Groves, 1979] to the upper limit set by maximum aerobic metabolic rate (R_A : Fry, 1947). The R_S of fishes have been obtained using a variety of techniques, including repeated measurements on the same individual until a minimum rate of oxygen consumption is observed (Steffensen *et al.*, 1994; Ferry-Graham & Gibb, 2001), regressing metabolic rate and swimming speed relationships back to zero activity to obtain the y-intercept (Brett, 1964; Muir *et al.*, 1965) or *via* the use of paralytic agents to isolate minimum costs of organ function (Brill, 1979). More commonly, researchers measure routine or resting metabolic rates (R_R), which include the oxygen consumption of fishes exhibiting minor spontaneous activity (Beamish, 1964; Prosser, 1973). Active metabolic rate (R_A) is generally measured as the oxygen consumption at increments of enforced activity leading up to the maximum sustainable speed or after exhaustive exercise (Brett, 1965; Soofiani & Priede, 1985).

Multiple environmental and biological factors influence the metabolic rates of fishes. The former include temperature and salinity (Hettler, 1976; Moser & Hettler, 1989; Wuenschel *et al.*, 2004), dissolved oxygen (Fitzgibbon *et al.*, 2007) and photoperiod (Boef & Le Bail, 1999; Jonassen *et al.*, 2000). The interactive effects of temperature and dissolved oxygen have received considerable attention because of their spatial and temporal variability in aquatic systems (Taylor & Peck, 2004). Biological factors affecting metabolic rates of fishes include body mass (Brett & Groves, 1979; Clarke & Johnston, 1999), ontogeny (Oikawa *et al.*, 1991; Post & Lee, 1996), life history (Metcalf *et al.*, 1995), individual disposition (McCarthy, 2001), stress (Barton & Schreck, 1987) and nutritional condition (Alsop & Wood, 1997). Additionally, the assimilation and biochemical transformation of food, termed specific dynamic action (SDA), elevate oxygen consumption and reduce the energy available to an organism for other activities (Beamish, 1974; Secor, 2009).

Comparative methods have provided novel insights into the form–function–environment relationships of teleost metabolic systems and how they affect behaviour (Metcalf *et al.*, 1995), habitat utilization (Chapman *et al.*, 1995, 2002), distribution and movement (van Dijk *et al.*, 1999), tolerance to environmental variables (MacIsaac *et al.*, 1997; Pichavant *et al.*, 2001), interspecific, intraspecific and predator–prey interactions (Morris & North, 1984), aquaculture (Brougher *et al.*, 2005) and bioenergetics (Hartman & Brandt, 1995; Burke & Rice, 2002). Despite the rich literature on teleost metabolic physiology (Clarke & Johnston, 1999), however, such data are sparse for many managed neritic fishes such as teleosts of the family Sciaenidae that support valuable commercial and recreational fisheries along the U.S. east coast. Sciaenids occupy a myriad of habitats in freshwater, estuarine and reef-associated marine systems, but are most speciose in neritic waters, where species-specific ecomorphologies and microhabitats result in niche separation (Myers, 1960; Chao & Musick, 1977). Temperature, salinity and dissolved-oxygen levels in estuaries used by sciaenids are highly variable (Breitburg, 2002). Previous studies have demonstrated that sciaenid fishes are good candidates for comparative study by

virtue of their taxonomic, morphological and microhabitat diversity (Chao & Musick, 1977; Horodysky *et al.*, 2008a, b), but there has been little comparative study of their metabolic rates. This study therefore uses intermittent-flow respirometry to assess R_R in four sciaenid species and R_A and costs of transport (C) in two species.

MATERIALS AND METHODS

ANIMAL COLLECTION AND HUSBANDRY

Experimental and animal care protocols were approved by the College of William and Mary's Institutional Animal Care and Use Committee and followed all relevant laws of the U.S. Atlantic croaker *Micropogonias undulatus* L. (1766), spot *Leiostomus xanthurus* Lacépède 1802, northern kingfish *Menticirrhus saxatilis* (Bloch & Schneider 1801) and southern kingfish *Menticirrhus americanus* (L. 1758) were captured by hook and line (Table I). Animals were maintained in recirculating 1855 l aquaria at mean \pm s.e. $15 \pm 1^\circ$ C (winter) or $25 \pm 2^\circ$ C (summer) and fed a combination of frozen Atlantic menhaden *Brevoortia tyrannus* (Latrobe 1802), squid *Loligo* sp. and commercially prepared food (AquaTox flakes; Zeigler; www.zeiglerfeed.com) (Table I). Prior to each trial, subjects were isolated and fasted for 48 h to ensure complete gastric evacuation. At the conclusion of each trial, wild subjects were tagged with a small plastic identification tag (Hallprint Pty Ltd; www.hallprint.com) and released to the captive research population.

AUTOMATED INTERMITTENT-FLOW RESPIROMETRY

Automated intermittent-flow respirometry was used to determine the R_R of four sciaenid species and the R_A of *M. undulatus* and *L. xanthurus* (Steffensen, 1989). In this technique, a respirometer, submerged in a flow-through outer bath, experiences repeated cycles of two computer-driven flow regimes over c. 36–48 h: flow-through chamber ventilation (5–10 min), when fresh sea water from the outer bath is flushed through the metabolic chamber, and closed-chamber MO_2 recording (5–60 min) intervals, where flushing ceases, effectively sealing the respirometer (Fig. 1). Accordingly, intermittent-flow respirometry eliminates wash-out problems of traditional flow-through respirometry and avoids the carbon dioxide and metabolite accumulation issues that plague closed respirometry (Steffensen, 1989). Furthermore, this computer-driven technique records metabolic rates with high temporal resolution over several days without the constant presence of a researcher, facilitating high data yields with reduced potential for human movement and noise biasing MO_2 upwards (Steffensen, 2002).

TABLE I. Species, sample size (n) and individual mean (range in parentheses) mass (M) of four sciaenid fishes investigated in (a) resting metabolic rate (R_R) and (b) active metabolic rate experiments

Species	n	M (g)
(a)		
<i>Micropogonias undulatus</i>	42	254 (30–790)
<i>Leiostomus xanthurus</i>	39	90 (4–240)
<i>Menticirrhus saxatilis</i>	9	236 (105–475)
<i>Menticirrhus americanus</i>	6	211 (130–250)
(b)		
<i>Micropogonias undulatus</i>	15	274 (75–480)
<i>Leiostomus xanthurus</i>	12	121 (55–196)

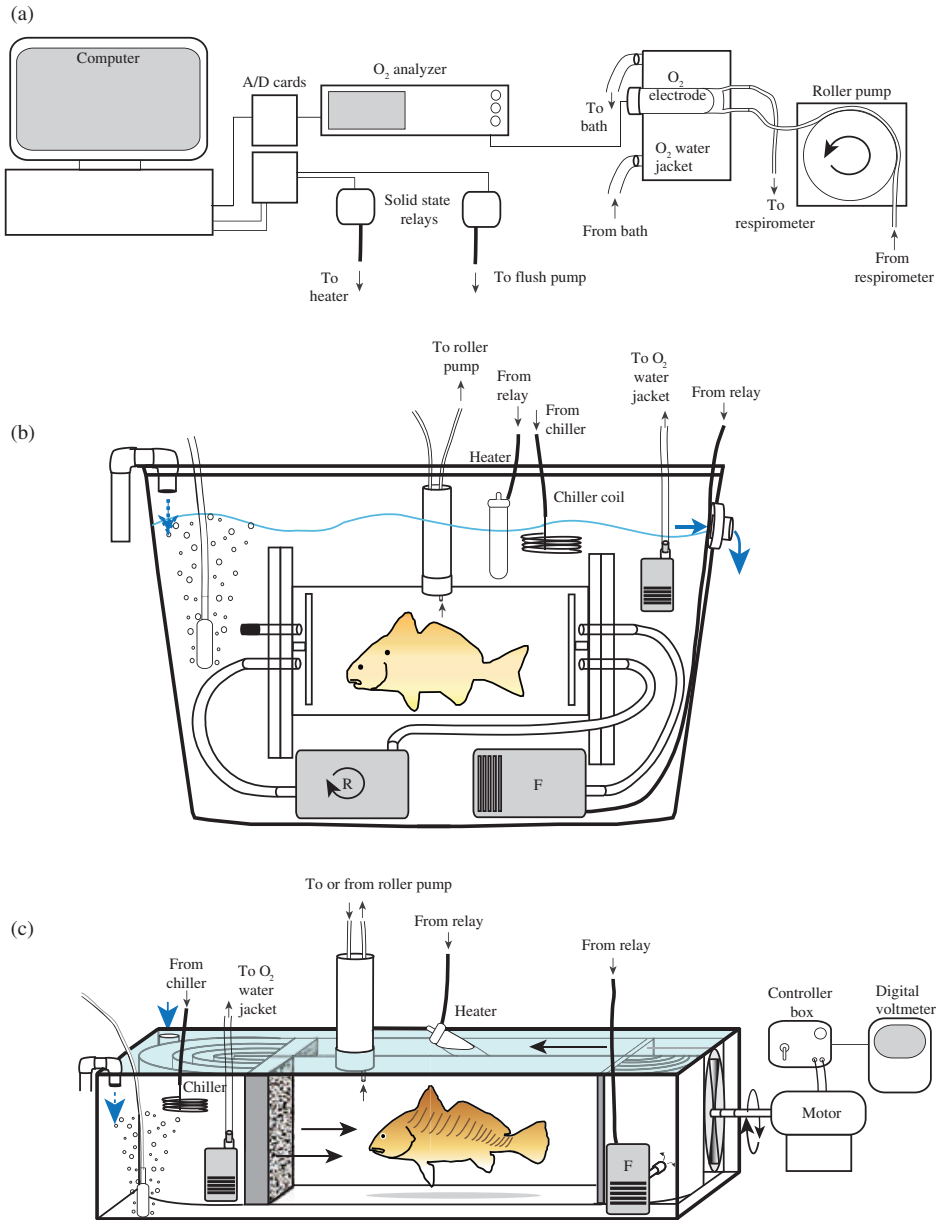


FIG. 1. Schematic representation of the metabolic chambers used in experiments. (a) Computing equipment and oxygen electrodes. (b) Experimental intermittent-flow respirometry chamber for resting metabolic rate (R_R) experiments (F, flushing pump; R, recirculating pump); the species illustrated is *Leiostomus xanthurus*. (c) Experimental intermittent-flow Blažka swim chamber for active metabolic rate (R_A) experiments (F, the flush pump); the species illustrated is *Micropogonias undulatus*. Filtered, oxygenated sea water was introduced to the system via the spigot on the left of (b) and (c) (--->) and exited the system via through-hull fitting (b) or standpipe (c).

RESTING METABOLIC RATE

The R_R were assessed as the M_{O_2} ($\text{mg kg}^{-1} \text{h}^{-1}$) of a thermally acclimated, unfed subject at low-level spontaneous motor activity. For each experiment (24–48 h), a subject was netted from its holding tank, weighed (g) and transferred depending on body mass (M) to a 0.35 or 7.40 l acrylic respirometer (Loligo Systems; www.loligosystems.com) that was submerged in a flow-through outer bath [Fig. 1(b)]. Temperature-controlled, aerated and filtered sea water was delivered to the bath with an approximate system-wide turnover rate of 20–30% h^{-1} (Dowd *et al.*, 2006). The M_{O_2} was measured during closed-respirometer intervals that were temporally adjusted until a subject extracted *c.* 20–30% of the dissolved oxygen from the sea water. At predetermined intervals, the respirometer was flushed with fresh sea water by a small pump submerged in the outer bath, forcing the oxygen-depleted water through a PVC chimney to be re-aerated and mixed in the outer bath. During both recording and flushing cycles, water within the respirometer was continually mixed by a small recirculating pump external to the chamber (Steffensen, 1989). Flushing and recirculating flows were diffused by baffles within the respirometer and the entire assembly was covered with black plastic to minimize visual disturbance. Respirometer turnover rates were 200–500% per flushing cycle. Collectively, R_R experiments were conducted at 10, 15, 20 and 25° C; when holding temperatures differed from experimental temperatures (difference < 5° C), acclimation occurred at the rate of *c.* 1° C h^{-1} .

CALCULATION OF OXYGEN UPTAKE

The partial pressure of oxygen (P_{O_2} , mm Hg) in respirometers was continuously measured with a polarographic electrode (Radiometer A/S; www.radiometer.dk) mounted in a water-jacketed cuvette (Loligo Systems) and connected to a digital oxygen meter (either Radiometer A/S or Cameron Instruments Company; www.cameroninstruments.com). Water temperature, time and P_{O_2} were oversampled, averaged to 1 s^{-1} to remove electronic noise, and recorded with a computerized data acquisition system by a custom DasyLab 7.0 worksheet interfacing with a QuattroPro 11.0 spreadsheet (www.adepscience.co.uk). The P_{O_2} values were converted to oxygen content ($\text{mg O}_2 \text{l}^{-1}$) for a given temperature and salinity following Richards (1965) and Dejours (1975). To help ensure the linearity of the rate of change of oxygen concentration with time, data from the first 60–180 s at the conclusion of the flush cycle were excluded from calculations. Oxygen uptake (M_{O_2} , mg h^{-1}) for a given measurement period was calculated from the time course of P_{O_2} change (Steffensen, 1984):

$M_{O_2} = V \Delta P_{O_2} \Delta t^{-1} \alpha^{-1}$, where V is the respirometer volume (l) corrected for fish volume, $\Delta P_{O_2} \Delta t^{-1}$ is the slope of the linear regression of P_{O_2} and time, and α is the oxygen solubility coefficient. The mass-specific R_R ($\text{mg O}_2 \text{kg}^{-1} \text{h}^{-1}$) were calculated by dividing absolute M_{O_2} (mg h^{-1}) by the M of the fish (in kg).

After being placed in the respirometer, most individuals displayed elevated metabolic rates for 1–3 h. These data were removed from analyses. Additionally, regressions of P_{O_2} and time with r^2 values < 0.9 were excluded from consideration (Hölker, 2003). The R_R for each species were calculated by fitting a normal distribution to the frequency distribution of M_{O_2} measurements (Steffensen *et al.*, 1994).

R_R ANALYSES

To investigate the effects of temperature on *M. undulatus* and *L. xanthurus* R_R , power models were fitted *via* non-linear least squares to data for each species pooled across temperature and compared results to model parameterized with a temperature covariate (following Kimura, 2008). Model fits were evaluated using an information theoretic approach (Akaike, 1973; Burnham & Anderson, 2002). As all experiments for both *Menticirrhus* species were conducted at 25° C, models for those species instead were parameterized with species as a covariate rather than temperature. All R_R data were modelled assuming additive error:

$$R_{R_i} = a_i M_i^{b_i} + \varepsilon_i, \quad (1)$$

where for the i th individual, R_{Ri} is the resting metabolic rate, M_i is body mass (kg), a_i is a constant, b_i is the shape parameter, ε_i is the error term, and $\begin{pmatrix} a_i \\ b_i \end{pmatrix} = \begin{pmatrix} \beta_{0a} + x_{iT}\beta_{Ta} \\ \beta_{0b} + x_{iT}\beta_{Tb} \end{pmatrix}$, where T designates either the temperature or species group covariate. Fitting models using this approach summarizes information in a manner that functionally relates population parameters to covariates of interest, such as temperature or species group (Kimura, 2008). One interpretation of this approach is that the covariates make adjustments to underlying average model parameters, while an alternative is that the covariates partition the study population into subsets that have their own model parameters (Kimura, 2008). This approach enables model-based inference, straightforward significance testing of covariates and efficient comparisons of several model parameterizations on the basis of model fit. Model comparisons were conducted separately using an information theoretic approach following Akaike's information criterion (AIC; Akaike, 1973; Burnham & Anderson, 2002):

$$y = -2 \ln(\hat{L}) + 2p, \quad (2)$$

where $y = \text{AIC}$, \hat{L} is the estimated value of the likelihood function at its maximum and p is the number of estimated parameters.

AIC is a parsimonious measure that strikes a balance between model simplicity and complex overparameterization (Burnham & Anderson, 2002). Accordingly, AIC provided a quantitative metric to evaluate the simplest, most likely estimates given the data. All statistical analyses were conducted using the software package *R* version 2.11.0 (R Development Core Team, 2010; www.r-project.org).

To place sciaenid data in context of other fishes, interspecific comparisons to other taxa were performed by first standardizing available oxygen consumption data from the experiments and the literature to absolute M_{O_2} ($\text{mg O}_2 \text{ h}^{-1}$), converting the oxygen consumption to 25°C where necessary via a global Q_{10} of 1.65 for fishes (White *et al.*, 2006) and regressing against M (kg). The M_{O_2} data of all species were allied graphically in three groups separated by energy demand, the end-members of which have been discussed by others (Brill, 1996; Fitzgibbon *et al.*, 2007). These three groupings were used in analyses that applied AIC to compare the fits of a power model parameterized with all species pooled into one group against one with a categorical energy demand covariate (Kimura, 2008).

ACTIVE METABOLIC RATE

For R_A experiments, the fishes were weighed, total length (L_T) and standard lengths (L_S) were measured and then fishes were immediately transferred to a modified Blažka-type (Blažka *et al.*, 1960) swimming respirometer [Fig. 1(c)]. Water temperature was maintained at $25.0 \pm 0.9^\circ \text{C}$, mean \pm s.e. Animals were allowed to acclimate to the chamber for 12 h with water velocity set to 0.5 body lengths (BL) s^{-1} during which time R_R were measured as described previously. During swimming trials, water flow within the chamber was increased for 20 min that included a 10 min flushing (open) phase and a 10 min (closed) recording phase. Water velocity was increased every 20 min, in steps that corresponded to 0.25 or 0.5 BL s^{-1} increments, until the subject was no longer able to continue sustained swimming and made contact with the rear chamber grate for >3 s twice within the same swimming speed measurement interval.

For R_A experiments, the relationship between swimming speed and M_{O_2} was investigated by fitting power functions of the form

$$M_{O_2} = a + bU^c, \quad (3)$$

where a , b and c are constants and U is the swimming speed (BL s^{-1}). The R_S were estimated by extrapolating the M_{O_2} relationship back to a constant U of 0 BL s^{-1} (*i.e.* the constant a

in equation 1) (Dewar & Graham, 1994). Maximum metabolic rate (R_A) was defined as each individual's metabolic rate at maximum swim speed.

Active metabolic rate experiments in which the oxygen consumption of a swimming individual is recorded repeatedly at increasing U may violate several fundamental assumptions of standard non-linear regression, including independence and constant variance (*i.e.* homoscedasticity) (Underwood, 2002). To consider each M_{O_2} measurement as independent within subjects is tantamount to pseudoreplication (Hurlbert, 1984); doing so may lead to biased parameter estimates (*i.e.* intercept, slope and shape parameters), s.e. and metrics of model fit (Littell *et al.*, 2006). Furthermore, R_A measurements may be more variable among subjects at higher v , resulting in violation of the regression assumption of homoscedasticity. Repeated-measures non-linear mixed-effects models that considered the within-individual autocorrelation (package nlme; Pinheiro & Bates, 2004) and weighted the data by the inverse of the variance at each level of the x -variable ($BL\ s^{-1}$) were therefore fitted to the sciaenid R_A data to account for repeated sampling of individuals, heteroscedastic variance and non-normally distributed error terms that violate regression assumptions of standard and mixed models. These mixed models contained fixed (U) and random variables (fishes). Subjects were a random sample from the wild population, thus 'fish' was modelled as a random variable. For each species, the best fitting covariance structure was objectively selected using an information theoretic approach (Burnham & Anderson, 2002) following AIC.

The costs of transport (C) and optimum swimming speeds (U_{opt}) were calculated separately for *M. undulatus* and *L. xanthurus* from the R_A model parameters and M_{O_2} data following Claireaux *et al.* (2006) and Videler (1993). For each individual, M_{O_2} at each U was converted from $mg\ O_2\ kg^{-1}\ h^{-1}$ to $J\ kg^{-1}\ h^{-1}$ using an oxycaloric coefficient of $13.6\ J\ mg\ O_2^{-1}$ (Elliott & Davison, 1975). Gross costs of transport (C_G ; $J\ kg^{-1}\ km^{-1}$) were determined by dividing each M_{O_2} by the U ($BL\ s^{-1}$) at which it was obtained and cancelling time units. A predictive line was calculated using the equation

$$C_G = \hat{a}U^{-1} + \hat{b}U^{(\hat{c}-1)}. \quad (4)$$

Net costs of transport (C_N ; $J\ kg^{-1}\ km^{-1}$) were determined by subtracting the R_S from each M_{O_2} , dividing by the U ($BL\ s^{-1}$) at which it was obtained, cancelling time units and plotting. Using parameter estimates from the best fitting power model, a predictive line was calculated from the equation

$$C_N = \hat{b}U^{(\hat{c}-1)}. \quad (5)$$

The optimum swimming speed (U_{opt} ; $BL\ s^{-1}$) was calculated according to the following equation:

$$U_{opt} = \{\hat{a}[(\hat{c} - 1)\hat{b}]^{-1}\}^{\hat{c}-1}. \quad (6)$$

Finally, C_{Nmin} and C_{Gmin} were calculated by inserting the U_{opt} for each species into equations (4) and (5) and cancelling time units.

RESULTS

The R_R of *M. undulatus* and *L. xanthurus* increase with M and temperature (Fig. 2 and Tables II and III). On the basis of ΔAIC values, the inclusion of temperature as a covariate resulted in substantially better fits to the *M. undulatus* and *L. xanthurus* R_R data than pooled models ignoring temperature (Table III). The null

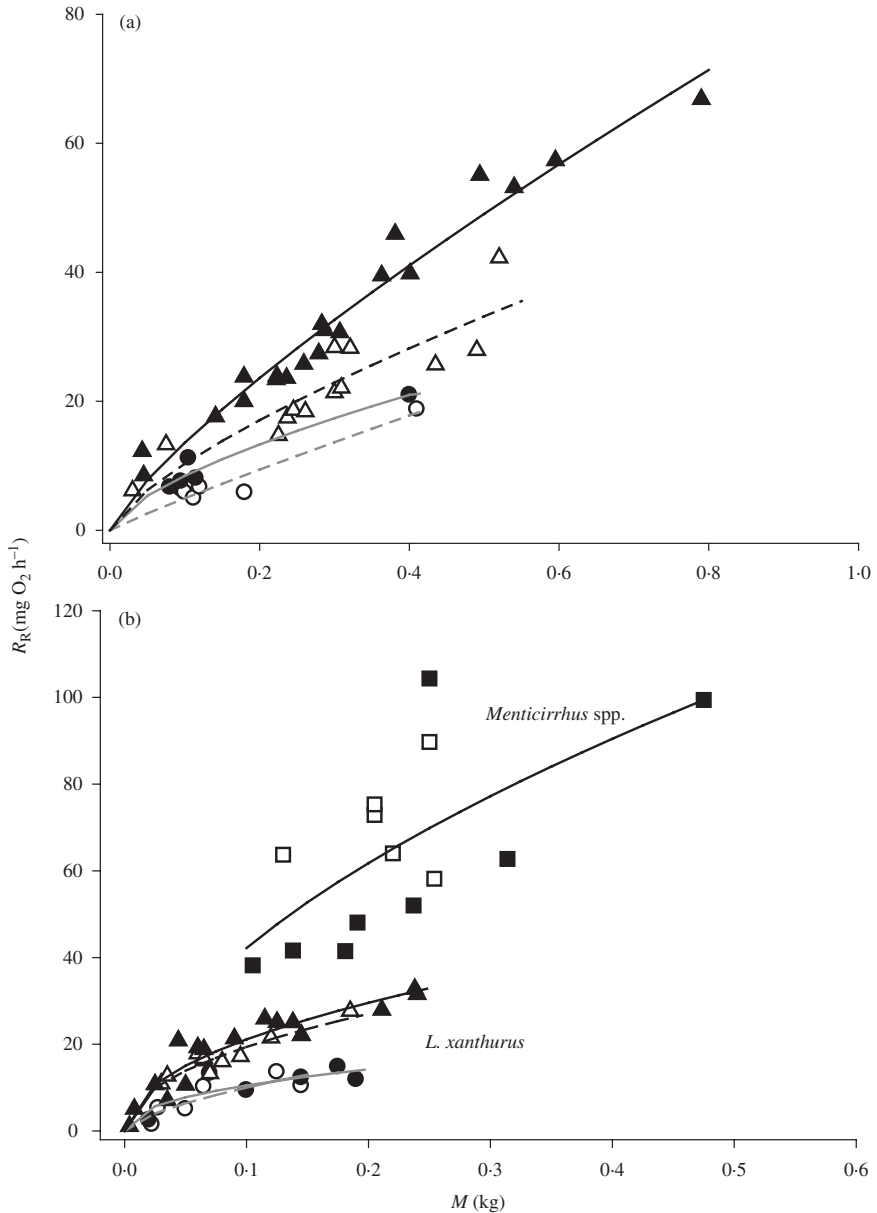


FIG. 2. Best fitting power equations (Tables II and III) fitted to the resting metabolic rates (R_R) of (a) *Micropogonias undulatus* and (b) *Leioostomus xanthurus* and *Menticirrhus* spp. For *M. undulatus* and *L. xanthurus*: at 10° C (—○—), 15° C (—●—), 20° C (—△—) and 25° C (—▲—). For *Menticirrhus* spp.: *Menticirrhus saxatilis* (□) and *Menticirrhus americanus* (■). The power function (—) is for the model pooling both species (best fit; Tables II and III).

model (pooled temperatures) received no empirical support. Estimates of the constant a in power functions fitted to each temperature separately for each species generally increased with temperature (*M. undulatus* mean $Q_{10} = 1.76$, *L. xanthurus* mean

TABLE II. Parameter estimates resulting from fitting power models parameterized to investigate the effects of temperature to resting metabolic rate (R_R) data using the approach described by Kimura (2008). Subscripts in the parameter column refer to temperature (T , °C) or species (sp., NK = *Menticirrhus saxatilis*, SK = *Menticirrhus americanus*). For pooled models, s.e. are presented for the estimates. For Kimura models, values in the estimates column are presented as the difference from the reference group (R), and s.e. captures the precision of the change from the reference group for a given covariate level. P -values are associated with tests evaluating whether each parameter estimate is statistically different from zero. Δ AIC was calculated by subtracting each model's AIC from the best fitting model's AIC (Δ AIC = 0 denotes best fit). Models with Δ AIC < 2 have strong support, those with Δ AIC > 10 have little to no support (Burnham & Anderson, 2002). Bold AIC values indicate the best fitting models

Species	Parameter	Estimate \pm s.e.	t	P	AIC	Δ AIC
<i>Micropogonias undulatus</i>	Pooled _T				299.4	56.7
	a	83.18 \pm 7.09	11.73	<0.001		
	b	0.95 \pm 0.08	11.28	<0.001		
	Kimura_T				242.7	0
	a_{10} (R)	41.33 \pm 15.66	2.64	<0.05		
	a_{15}	-3.05 \pm 19.47	-0.16	>0.05		
	a_{20}	13.47 \pm 17.17	0.79	>0.05		
	a_{25}	43.94 \pm 16.10	2.73	<0.05		
	b_{10} (R)	0.92 \pm 0.27	3.44	<0.01		
	b_{15}	-0.26 \pm 0.33	-0.81	>0.05		
	b_{20}	-0.20 \pm 0.29	-0.67	>0.05		
b_{25}	-0.12 \pm 0.27	-0.45	>0.05			
<i>Leiostomus xanthurus</i>	Pooled _T				246.3	47.7
	a	56.84 \pm 11.10	5.12	<0.001		
	b	0.52 \pm 0.09	5.85	<0.001		
	Kimura_T				198.9	0
	a_{10} (R)	44.49 \pm 26.43	1.68	>0.05		
	a_{15}	-15.75 \pm 29.16	-0.54	>0.05		
	a_{20}	14.02 \pm 29.48	0.48	>0.05		
	a_{25}	20.12 \pm 27.33	0.74	>0.05		
	b_{10} (R)	0.65 \pm 0.25	2.61	<0.05		
	b_{15}	-0.21 \pm 0.32	-0.66	>0.05		
	b_{20}	-0.17 \pm 0.26	-0.63	>0.05		
b_{25}	-0.16 \pm 0.25	-0.64	>0.05			
<i>Menticirrhus</i> spp.	Pooled_{sp}				122.2	0
	a	149.71 \pm 38.55	3.88	<0.01		
	b	0.55 \pm 0.18	3.10	<0.01		
	Kimura_{sp}				122.8	0.6
	a_{NK} (R)	166.05 \pm 45.79	3.62	<0.01		
	a_{SK}	-71.89 \pm 79.66	-0.90	>0.05		
	b_{NK}	0.68 \pm 0.21	3.31	<0.01		
b_{SK}	-0.50 \pm 0.48	-1.03	>0.05			

$Q_{10} = 1.78$), but the scaling parameter b did not. Parameter estimates for *L. xanthurus* at 10 and 15°C were imprecise due to high variability in measured R_R values and low sample size. On the basis of Δ AIC values, a model parameterized with a

TABLE III. Summary of R_R equations for *Micropogonias undulatus* and *Leiostomus xanthurus* fitted separately to temperatures, and pooled for *Menticirrhus* spp. s.e. are reported in parentheses following parameter estimates. Best fitting models based on analyses summarized in Table II are presented

Species	R_R equation
<i>Micropogonias undulatus</i>	$R_{R10C} = 41.3(\pm 7.9)M^{0.92(\pm 0.14)}$ $R_{R15C} = 38.3(\pm 5.6)M^{0.65(\pm 0.09)}$ $R_{R20C} = 54.8(\pm 9.0)M^{0.72(\pm 0.15)}$ $R_{R25C} = 85.3(\pm 3.6)M^{0.78(\pm 0.04)}$
<i>Leiostomus xanthurus</i>	$R_{R10C} = 44.5(\pm 23.7)M^{0.65(\pm 0.22)}$ $R_{R15C} = 28.7(\pm 12.9)M^{0.44(\pm 0.22)}$ $R_{R20C} = 58.5(\pm 8.3)M^{0.48(\pm 0.06)}$ $R_{R25C} = 64.6(\pm 8.3)M^{0.48(\pm 0.06)}$
<i>Menticirrhus</i> spp.	$R_{Rall} = 149.7(\pm 38.5)M^{0.54(\pm 0.18)}$

species covariate (for *M. saxatilis* and *M. americanus*) did not improve fit relative to a model pooling both *Menticirrhus* species; both species were thus combined into a pooled model (Table III). At 25° C, *Menticirrhus* spp. demonstrated an R_R roughly double that of *M. undulatus* and *L. xanthurus* and a shape parameter intermediate between the species (Table III).

For the analysis of sciaenid energy demand in the context of other fishes, the power model incorporating a covariate for energy demand (three levels) provided a superior

TABLE IV. Comparison of a power model fitted to pooled sciaenid energy demand data from this study and literature values *v.* a model parameterized to include a covariate for energy demand (three levels). For the pooled model, s.e. are presented for the estimates. For the Kimura model, values in the estimates column are presented as the difference from the reference group (R), and s.e. captures the precision of the change from the reference group for a given covariate level. *P*-values are associated with tests evaluating whether each parameter estimate is statistically different from zero. Δ AIC was calculated by subtracting each model's AIC from the best fitting model's AIC (Δ AIC = 0 denotes best fit). Models with Δ AIC < 2 have strong support, those with Δ AIC > 10 have little to no support (Burnham & Anderson, 2002). Bold AIC values indicate best fitting model

Model	Parameter	Estimate \pm s.e.	<i>t</i>	<i>P</i>	AIC	Δ AIC
All species	<i>a</i>	238.20 \pm 8.03	29.66	<0.01	2380.5	184.6
pooled	<i>b</i>	0.88 \pm 0.03	29.49	<0.01		
Kimura, three groups	A _{HED} (R)	345.70 \pm 7.93	43.55	<0.01	2195.9	0
	A _{EED}	-153.40 \pm 30.22	-5.08	<0.01		
	A _{SED}	-260.70 \pm 29.67	8.79	<0.01		
	B _{HED} (R)	0.54 \pm 0.02	23.51	<0.01		
	B _{EED}	0.18 \pm 0.18	1.04	>0.05		
	B _{SED}	0.19 \pm 0.25	0.77	>0.05		

EED, elevated-energy-demand species; HED, high-energy-demand species; SED, standard-energy-demand teleosts.

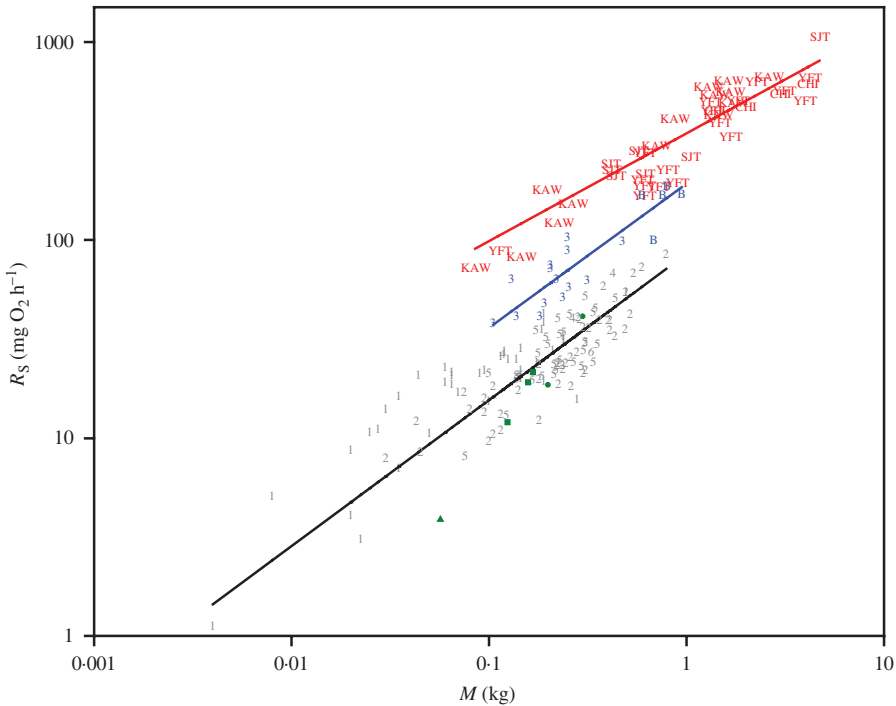


FIG. 3. Interspecific comparison of the relationship between resting metabolic rate (R_S) and mass (M) of three groups of fishes categorized by energy demand: standard-energy-demand fishes (—) ($R_S = 85 \times M^{0.74}$), elevated-energy-demand fishes (—) ($R_S = 192 \times M^{0.72}$) and high-energy-demand fishes (—) ($R_S = 345 \times M^{0.54}$). All data were standardized to 25°C via a Q_{10} of 1.65 (White *et al.*, 2006). Standard energy demand teleosts include: 1, *Leiostomus xanthurus*; 2, *Micropogonias undulatus*; 4, *Cynoscion regalis* (A. Z. Horodysky, unpubl. data); 5, *Cynoscion nebulosus* (Vetter, 1982; A. Z. Horodysky, unpubl. data); 6, *Argyrosomus japonicus* (Fitzgibbon *et al.*, 2007); [●], *Oncorhynchus mykiss* (Evans, 1990); [▲], *Salmo trutta* (Sloman *et al.*, 2000); [■], *Gadus morhua* (Schurmann & Steffensen, 1997). Elevated energy demand teleosts include: 3, *Menticirrhus* spp. (this study) and B, *Pomatomus saltatrix* (P. G. Bushnell, unpubl. data). High energy demand teleosts include: SJK, *Katsuwonus pelamis*; YFT, *Thunnus albacares*; KAW, *Euthynnus affinis* and CHI, *Coryphaena hippurus* (Benetti *et al.*, 1995; Brill, 1979; Dewar & Graham, 1994; Sepulveda & Dickson, 2000). Note that axes are log-transformed for graphical purposes, but data were not transformed for model fitting.

fit when compared to a model that pooled all species (see Δ AIC, Table IV). *Leiostomus xanthurus* and *M. undulatus* have R_R similar to a wide range of teleosts with fairly standard energy demands (Fig. 3). The metabolic rates of fishes with comparatively elevated energy demands including *Menticirrhus* spp. and bluefish *Pomatomus saltatrix* (L. 1766) were roughly double those of standard-energy-demand fishes. The metabolic rates of high-energy-demand species (Brill, 1996) such as tunas and the common dolphinfish *Coryphaena hippurus* L. 1758 were about nearly double those of elevated-demand-fishes and about four times higher than those of most teleosts. The estimated shape parameter b was lowest in the high-demand fishes and roughly equivalent in elevated and standard-energy-demand teleosts.

Relative to standard non-linear regression, non-linear mixed-effects models fitted to the *M. undulatus* and *L. xanthurus* R_A data that accounted for repeated measures

TABLE V. Summary statistics for non-linear mixed-effects models fitted *via* maximum likelihood to (a) *Micropogonias undulatus* and (b) *Leiostomus xanthurus* active metabolic rate (R_A) data obtained at 25° C. Models were of the form: $M_{O_2} = a + bU^c$ (equation 3). Standard non-linear models did not account for any repeated measures or heteroscedasticity (NO). Repeated measures were considered only where indicated (RM), and covariance structures were default (D), autoregressive first-order [AR(1)], autoregressive moving average (ARMA) and compound symmetry (CS). For Akaike's information criterion (AIC) (equation 2) the lower value denotes better fit. Δ AIC was calculated by subtracting each model's AIC from the best fitting model's AIC (Δ AIC = 0 denotes best fit). Models with Δ AIC < 2 have strong support, those with Δ AIC > 10 have little to no support (Burnham & Anderson, 2002). The AIC values in bold indicate the model with best fit

Model	$a \pm$ S.E.	$b \pm$ S.E.	$c \pm$ S.E.	AIC	Δ AIC
(a)					
NO	133.1 \pm 43.3	88.7 \pm 28.0	1.34 \pm 0.17	1910.0	69.3
RM, D	139.7 \pm 24.5	82.1 \pm 17.6	1.39 \pm 0.13	1864.2	23.5
RM, AR(1)	126.0 \pm 27.2	93.5 \pm 24.8	1.32 \pm 0.16	1841.5	0.8
RM, ARMA	115.3 \pm 28.4	106.1 \pm 28.0	1.23 \pm 0.16	1840.7	0
RM, CS	130.8 \pm 24.8	88.0 \pm 20.6	1.34 \pm 0.14	1863.7	23
(b)					
NO	13.0 \pm 116.4	246.4 \pm 95.4	0.89 \pm 0.17	2085.3	89.7
RM, D	193.1 \pm 23.0	69.8 \pm 15.6	1.60 \pm 0.12	2005.0	9.4
RM, AR(1)	167.2 \pm 41.2	117.1 \pm 40.2	1.26 \pm 0.16	1995.8	0.2
RM, ARMA	176.6 \pm 37.8	108.0 \pm 36.5	1.31 \pm 0.18	1995.6	0
RM, CS	193.0 \pm 22.1	67.6 \pm 15.5	1.66 \pm 0.12	2007.4	11.8

(by specifying the within-individual covariance) and adjusted for heteroscedasticity improved model fit, satisfied normality of the residual error and reduced s.e. of parameter estimates including the y -intercept (Table V and Fig. 4). Specifically, autoregressive first-order [AR(1)] and autoregressive moving average (ARMA) covariance models significantly outfit all other models considered for both *L. xanthurus* and *M. undulatus*. ARMA models slightly outfit AR(1) models (Table V); estimates from the former were therefore used in subsequent calculations. For both species, ARMA model y -intercepts fit neatly within the 95% C.I. of the R_R at 25° C, calculated for each species by substituting the mean mass of individuals used in the swim trials into equation 1. The maximum R_A were 869.2 mg O₂ kg⁻¹ h⁻¹ for *M. undulatus* and 1274.9 mg O₂ kg⁻¹ h⁻¹ for *L. xanthurus*, which suggest factorial metabolic scopes ($R_A R_R^{-1}$) of 7.2 and 10.6 times R_S , respectively (Table VI). It should be noted, however, that *M. undulatus* in this study were roughly 1.5–2 times greater in M than *L. xanthurus*.

The C_G and C_N were calculated from the *M. undulatus* and *L. xanthurus* R_A data and equation 3 parameters resulting from ARMA models (Table VI). For both species, C_G assumed a J-shaped curve with initial high costs and subsequently reduced costs at intermediate swimming speeds (Fig. 5). The optimal swimming speeds (U_{opt}), calculated from equation 6, were 3.5 BL s⁻¹ for *M. undulatus* and 3.6 BL s⁻¹ for *L. xanthurus*. The C_{Nmin} were 0.54 J kg⁻¹ BL⁻¹ for *M. undulatus* and *L. xanthurus*, while the C_{Gmin} were 0.66 and 0.79 J kg⁻¹ BL⁻¹, respectively.

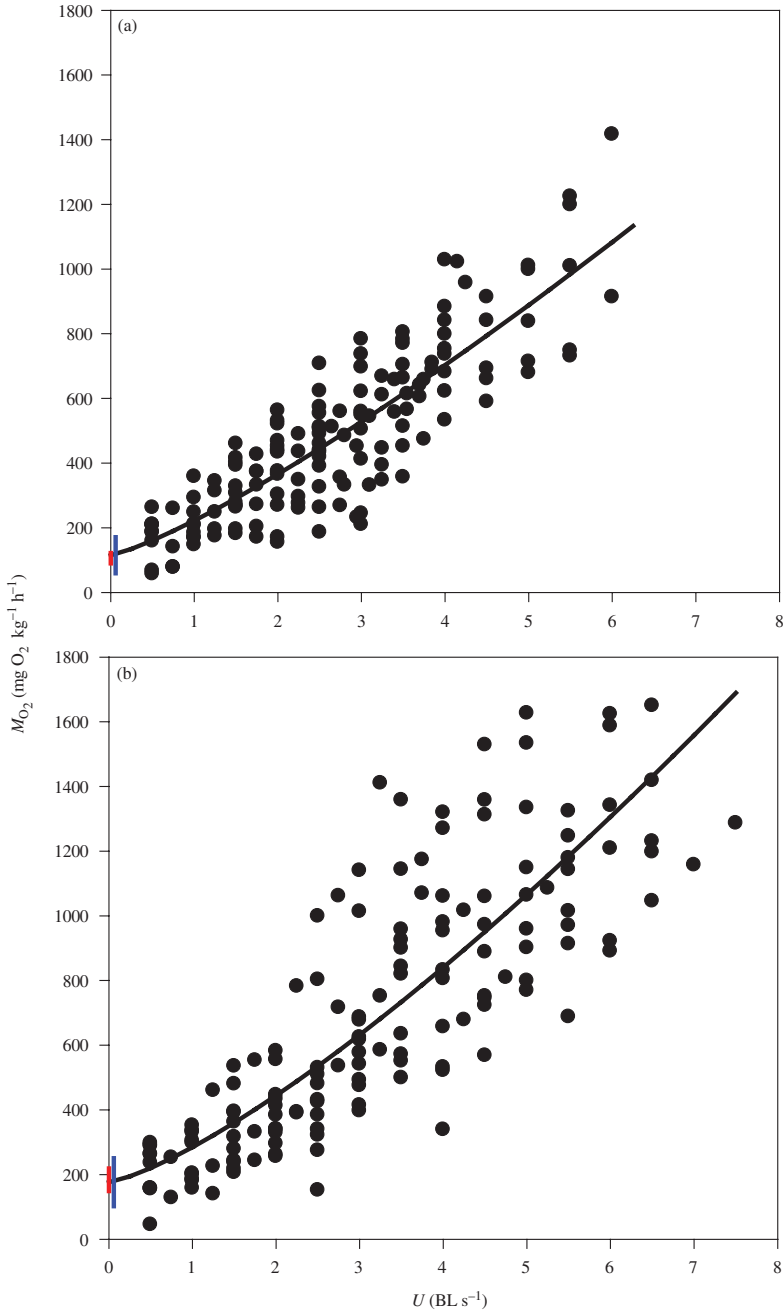


FIG. 4. Oxygen consumption (M_{O_2}) as a function of swimming speed (U) of (a) *Micropogonias undulatus* ($n = 15$) and (b) *Leiostomus xanthurus* ($n = 12$) at $25^\circ C$. The curve represents the best fitting equation (equation 3). For both species, repeated-measures linear mixed-effects models using the ARMA covariance matrix best fit the active metabolic rate (R_A) data; corresponding parameter estimates and AIC model fits are given in Table V. Red lines denote 95% c.i. of resting metabolic rate (R_R) for a fish with mean mass (M) of all swum individuals (equation 1) and blue lines denote 95% c.i. of y-intercept estimated by the best fitting ARMA model (equation 3) for each species (Table V).

TABLE VI. Summary of the estimated standard metabolic rate (R_S) \pm s.e., mean resting metabolic rates (R_R), maximum active metabolic rate (R_A), metabolic scope, optimum swimming speeds (U_{opt}), minimum net costs of transport (C_{Nmin}) and minimum gross costs of transport (C_{Gmin}) for *Micropogonias undulatus* and *Leiostomus xanthurus* at 25°C. *Micropogonias undulatus* in this study were roughly 1.5–2 times greater in mass (M) than *L. xanthurus* (Table I). The R_S values were estimated by obtaining the y-intercept (0 BL s^{-1}) of the best fitting R_A power function (equation 3), while mean R_R was calculated by inserting the mean R_A experimental subject M into the appropriate 25°C equations from Tables II and III. Metabolic scope was calculated as maximum $R_A R_R^{-1}$

Parameter	<i>M. undulatus</i>	<i>L. xanthurus</i>
R_{S25C} estimate (mg O ₂ kg ⁻¹ h ⁻¹)	115.3 \pm 28.4	176.6 \pm 37.8
Mean R_{R25C} (mg O ₂ kg ⁻¹ h ⁻¹)	113.3 \pm 8.2	194.1 \pm 17.9
Maximum R_A (mg O ₂ kg ⁻¹ h ⁻¹)	869.2 \pm 71.7	1274.9 \pm 55.3
Scope (mg O ₂ kg ⁻¹ h ⁻¹)	7.5	7.2
U_{opt} (BL s ⁻¹)	3.5	3.6
C_{Nmin} (J kg ⁻¹ BL ⁻¹)	0.54	0.54
C_{Gmin} (J kg ⁻¹ BL ⁻¹)	0.66	0.79

DISCUSSION

RESTING METABOLISM

The superior fit of models containing a covariate for temperature relative to models that pooled across temperature demonstrate that the R_R of *M. undulatus* and *L. xanthurus* increase with M and temperature, as do those of a wide variety of species. By definition, R_R measurements overestimate R_S due to the spontaneous

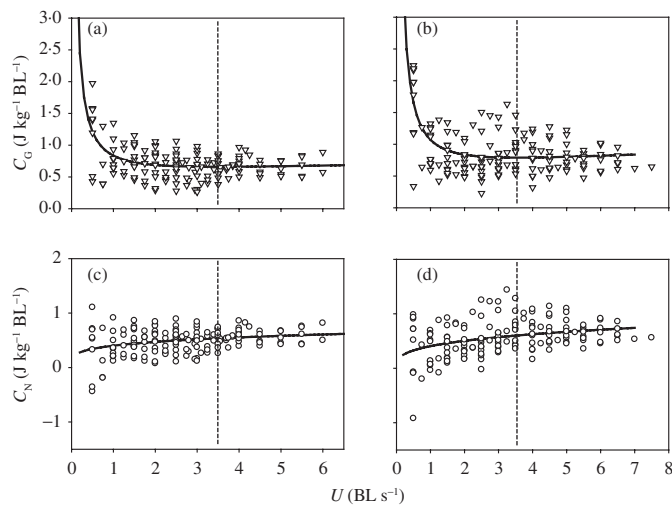


FIG. 5. The (a), (b) gross costs of transport (C_G) and (c), (d) net costs of transport (C_N) for (a), (c) *Micropogonias undulatus* ($n = 15$) and (b), (d) *Leiostomus xanthurus* ($n = 12$) swum (U) at 25°C. —, predicted values calculated from parameter estimates from equations 4 and 5. \vdots , C_{Gmin} and C_{Nmin} at the U_{opt} of each species, calculated from equation 6.

movements of subjects to maintain position and posture. Nonetheless, these results agree with previous investigations of R_R in larvae and juveniles of both species (Hoss *et al.*, 1988; Moser & Hettler, 1989). Interspecific comparisons to a wide array of taxa suggest that *M. undulatus* and *L. xanthurus* have R_R that are very typical for most freshwater, anadromous and marine teleosts (Fig 3). When compared to other taxa, the R_R of *M. undulatus* and *L. xanthurus* align with the R_R of rainbow trout *Oncorhynchus mykiss* (Walbaum 1792), brown trout *Salmo trutta* L.1758 and Atlantic cod *Gadus morhua* L.1758, as well as several other sciaenid species including weakfish *Cynoscion regalis* (Bloch & Schneider 1801) (A. Z. Horodysky, unpubl. data), silver seatrout *Cynoscion arenarius* Ginsburg 1930, spotted seatrout *Cynoscion nebulosus* (Cuvier 1830) (Vetter, 1982) and mulloway *Argyrosomus japonicus* (Temminck & Schlegel 1843) (Fitzgibbon *et al.*, 2007). At 25° C, the metabolic rates of most teleosts were roughly a quarter of those observed in high-energy-demand species such as *Thunnus* spp. and *C. hippurus* (Brill, 1996).

An unexpected finding in this study was that the energy demand of *Menticirrhus* spp. roughly doubles that of most fishes with standard energy demands (including *M. undulatus* and *L. xanthurus*) and is *c.* 1.8 times lower than the high-energy-demand fishes (*i.e.* *Thunnus* spp.) (Table IV). The R_R of *Menticirrhus* spp. were similar to those of *P. saltatrix* (P. G. Bushnell, unpubl. data; Fig 3.), a highly active, fast-growing coastal pelagic species. *Menticirrhus* spp., *L. xanthurus* and *M. undulatus* have been grouped by some authors on the basis of life-history strategies (longevity and maximum body size, and rapid maturity) that are intermediate relative to other sciaenids (Waggy *et al.*, 2006), but interesting differences in habitat use and morphology exist among the species. *Menticirrhus* spp. almost exclusively use median and paired fin gaits in captivity (A. Z. Horodysky, pers. obs.), which may provide enhanced mobility in the high wave-energy and oxygen-saturated littoral zones that the species frequents. By contrast, *M. undulatus* and *L. xanthurus* display an array of fin propulsion mechanisms and inhabit a myriad of aquatic habitats (Chao & Musick, 1977). It is likely that the elevated growth rate of *Menticirrhus* spp. (Miller *et al.*, 2002) is linked to their substantially elevated R_R relative to other sciaenids. It has been postulated that high maximum R_A allow high growth rates (Brill, 1996), which are supported by higher rates of oxygen extraction and delivery made possible by larger gill surface areas (Pauly, 1981) which in turn appear linked to elevated R_S (Brill, 1987, 1996; Boggs & Kitchell, 1991). While gill surface areas have not been examined in sciaenids, *Menticirrhus* spp. demonstrate substantially higher heart rates than either *M. undulatus* or *L. xanthurus* (R. W. Brill and P. G. Bushnell, unpubl. data), suggesting high oxygen and metabolite distribution capabilities that could support the elevated energy demands and R . The physiological mechanisms and ecological consequences of elevated R_R in *Menticirrhus* spp. remain unclear, and further study within the genus is clearly warranted.

ACTIVE METABOLISM

The R_A and C in fishes are typically determined by measuring M_{O_2} of individuals at increasing U , yet few studies have accounted for the within-individual autocorrelation or heteroscedastic variance that generally results from such experiments. Failure to consider these fundamental violations of regression assumptions can result in biased or invalid parameter estimates, s.e. and metrics of fit as well as inflated

probability of type I errors (falsely concluding significance; Underwood, 2002). Individually fitting power functions to each fish and averaging parameter estimates would suffer from autocorrelated within-individual errors.

The consideration of whether to treat fishes as a fixed or random effect in modelling procedures strongly affects the resulting scope of inference. Considering 'fish' as a fixed effect (*i.e.* not specifying it as a random effect in the model) limits inference to specific experimental subjects and does not allow inferences to be applied to the population from which samples were obtained (Davidian & Giltinan, 1995). By contrast, mixed-effects models account for variability in the global population and increase the scope of inference to the larger wild population from which subjects were sampled by treating subjects as truly random samples of the larger population (Littell *et al.*, 2006).

In this study, repeated-measures non-linear mixed-effects models with AR(1) and ARMA covariance structures that accounted for heteroscedasticity applied to the *M. undulatus* and *L. xanthurus* R_A data significantly improved model fits and reduced parameter S.E. relative to standard non-linear regression. Both AR(1) and ARMA covariance structures assume that the correlation between observations is a function of their lag in time; adjacent observations (in this case, M_{O_2} at adjoining U) are more likely to be strongly correlated than those taken further apart (*i.e.* at dissimilar U) within an individual (Pinheiro & Bates, 2004). ARMA models include an additional moving average smoothing parameter and may outperform AR(1) models when data are particularly noisy (Pinheiro & Bates, 2004), such as in R_A experiments with wild fishes that may vary in body condition and size. Information Theoretic model selection *via* AIC provides an objective balance between model simplicity (fewer parameters) and fit; models are penalized for additional parameters (Burnham & Anderson, 2002). Collectively, these methods hold great potential for improving the analyses of data resulting from R_A and other repeated-measures metabolic experiments.

The R_R and R_S converge when within-chamber activity is low. Regressing ARMA power performance curves to zero U (*i.e.* y -intercept) generated estimates of R_S that neatly aligned within the 95% C.I. of experimental measurements of R_R for *M. undulatus* and *L. xanthurus* (Table VI and Fig. 4). The lack of significant differences in these two complementary techniques demonstrates that the R_S estimated in this study are probably close to true R_S and confirm the validity of the approach and the utility of repeated-measures methods for R_S estimation from R_A experiments. Potential increases in M_{O_2} above values expected at low swimming speeds due to stress and spontaneous activity (Bushnell *et al.*, 1984), however, may still hamper the estimation of R_S from R_A experiments using these and other analytical methods.

Swimming respirometry revealed that *L. xanthurus* had higher maximum R_A and broader metabolic scopes than *M. undulatus*. It should be noted, however, that *M. undulatus* in this study were roughly 1.5–2 times greater in M than *L. xanthurus*, thus some of this effect may be due to differences in M . The maximum R_A of *M. undulatus* and *L. xanthurus* were 2.3 and 3.5 times higher than those of cultured *A. japonicus*, a Pacific sciaenid (Fitzgibbon *et al.*, 2007), comparable to those of sockeye salmon *Oncorhynchus nerka* (Walbaum 1792) corrected to 25° (Brett, 1965), but less than half of the R_A of yellowfin tuna *Thunnus albacares* Bonaterre 1788 (Korsmeyer *et al.*, 1996). Factorial scopes of *M. undulatus* (7.5) and *L. xanthurus* (7.2) were within the range for *O. nerka* (4–16; Brett, 1965), similar to those observed in *T. albacares* (11.5; Korsmeyer *et al.*, 1996), and higher than those

observed in Atlantic cod *Gadus morhua* L. 1758 (3.1; Schurmann & Steffensen, 1997), *O. mykiss* (3.9; Bushnell *et al.*, 1984), Pacific yellowtail *Seriola lalandi* Valenciennes 1833 (4.0; Clark & Seymour, 2006) and *A. japonicus* (5; Fitzgibbon *et al.*, 2007). These results suggest that the metabolic scopes of *M. undulatus* and *L. xanthurus* are typical for standard-energy-demand fishes of similar morphologies and life styles. Finally, U_{opt} values for *M. undulatus* (3.5 BL s⁻¹) and *L. xanthurus* (3.6 BL s⁻¹) were higher than those of several sciaenids including red drum *Sciaenops ocellatus* (L. 1766) (3.0 BL s⁻¹), *C. nebulosus* (2.7 BL s⁻¹) and *A. japonicus* (1.3 BL s⁻¹) (Videler, 1993; Fitzgibbon *et al.*, 2007). Additionally, U_{opt} probably approximates routine swimming velocity in highly migratory fishes, but the routine swimming velocities of more sedentary species are probably much less than U_{opt} (Videler, 1993; Steinhausen *et al.*, 2005). Interspecific comparisons of U_{opt} are, however, complicated by the use of numerous testing protocols (U increments and durations), study temperatures, individual status (wild *v.* culture), body conditions and sizes and variable life histories (Fitzgibbon *et al.*, 2007).

The R_A in fishes range widely due to diverse biochemical, morphological and physiological adaptations among taxa, allowing insights into the bounds of energy requirements and C . The C_G is a measure of the energy required to travel a unit difference and frequently assumes a J-shaped function with high initial C when R_S dominates total M_{O_2} , low intermediate C and increasing values above U_{opt} due to steeply increasing hydrodynamic resistance with U . The C_N is a measure of the C excluding R_S ; the proportional contribution of C_N to C_G thus increases with increasing U . The C_G and C_N of *M. undulatus* and *L. xanthurus* are classic examples of this pattern, although increases above U_{opt} are slight (Fig. 5). The C_G for *L. xanthurus* and *M. undulatus* appear only marginally affected over a broad range of intermediate and higher U (fairly unsubstantial C increases with U), typical of low-drag swimming and foraging generalist fishes that have adapted for swimming performance at higher U (Pettersson & Hedenström, 2000). Juvenile *M. undulatus* and *L. xanthurus* may not move great distances within estuarine nursery habitats at 25° C; however, adults of these and many other fishes undertake pronounced offshore migrations when inshore and estuarine temperatures decline to 10–15° C (Murdy *et al.*, 1997). Future R_A experiments conducted at 10 and 15° C will permit the estimation of the energetic costs of these winter migrations.

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