

THE EFFECTS OF BODY SIZE, OXYGEN TENSION AND MODE OF LIFE ON THE OXYGEN UPTAKE RATES OF POLYCHAETES*

SANDRA E. SHUMWAY

N.E.R.C. Unit of Marine Invertebrate Biology, Marine Science Laboratories,
Menai Bridge, Gwynedd, Wales and
Portobello Marine Laboratory, University of Otago, Dunedin, New Zealand

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Abstract—1. Oxygen consumption rates were monitored in eight species of marine polychaetes with respect to size and oxygen tension.
2. The slopes of the log-log plots relating body size to oxygen consumption ranged from 0.61–0.69.
3. All species were found to be oxygen-dependent over the range 5–100% air saturation.
4. Errant polychaetes were found to have a respiratory rate 2.4 times as high as sedentary polychaetes.

INTRODUCTION

The relationship between metabolic rate and body size has drawn considerable attention (Bertalanffy, 1951, 1957; Hemmingsen, 1960; Zeuthen, 1947, 1953), as has the effect of declining oxygen tension on metabolic rate (Tang, 1933; Mangum & van Winkle, 1973); however, the physiological/ecological implications of these parameters are not so well documented.

It is possible to characterize individual species by specific metabolic levels, these levels being indicated by respiration rates (Nicol, 1960). Thus, respiration data collected under similar experimental conditions may be used to indicate physiological speciation (Sander, 1973).

Marine polychaetes are found in many different types of habitats and have varying life styles. It is the aim of this study to compare the metabolic responses of marine polychaetes and to relate these differences to species' habitat and/or life style.

MATERIALS AND METHODS

Specimens of *Arenicola marina* L., *Aphrodite aculeata* L., *Nereis virens* L. and *Nereis diversicolor* L. were collected from the Anglesey coast (U.K.). Specimens of *Abarenicola assimilis*, *Eulalia microphylla* Savigny 1818, *Glycera americana* Savigny 1818 and *Perenereis nuntia* Kinberg were collected from Otago Harbor (N.Z.). All animals were maintained at 10°C for at least 1 week prior to use in experiments, and all experiments were conducted at 10°C.

Oxygen consumption was monitored using a Radiometer oxygen electrode (Radiometer E5046) connected via a Radiometer PHM 71 Mk2 pH meter to a Smith's servoscribe chart recorder as described previously (Crisp *et al.*, 1978). The worms were placed in blackened experimental chambers and casual observations indicated that they remained inactive during the experiments.

The effect of declining oxygen tension on the oxygen consumption of the worms was determined by allowing the animals to deplete the oxygen supply in the experimen-

tal chamber. The weight-specific oxygen consumption rate of the animal was then plotted against percent air saturation.

RESULTS

Figures 1 and 2 show the relationship between oxygen consumption and tissue dry weight for eight species of polychaetes. Oxygen consumption, expressed as ml O₂ hr⁻¹ is given by the following equation:

$$Y = aX^b$$

where Y is oxygen consumption, X is the dry weight in grams, b is the slope of a plot of log O₂ consumption against log dry weight and a is a proportionality factor. The linear regression equations are given in Figs 1 and 2 and Table 1. For comparative purposes Table 1 also includes the relationships between oxygen consumption and body weight for several other species of polychaetes. In many cases it was necessary to recalculate the data as presented by other authors and in some cases percent dry weight of tissue had to be estimated.

Figures 3 and 4 show the effect of declining O₂ tension on respiratory rate for the eight species studied. In all species the rate of oxygen consumption was almost totally dependent on the oxygen concentration of the external medium.

DISCUSSION

Respiration and body size

That respiration is related to body size is well established; however, the manner in which they are related warrants some discussion. The relationship between metabolic rate and weight is usually expressed by the equation:

$$Y = aX^b$$

(see Results for explanation of terms).

The derivation and significance of b have long been points of discussion. Zeuthen (1947, 1953) states that

* Address for reprint requests: 71 Clifford Street, Taunton, Massachusetts 02780, U.S.A.

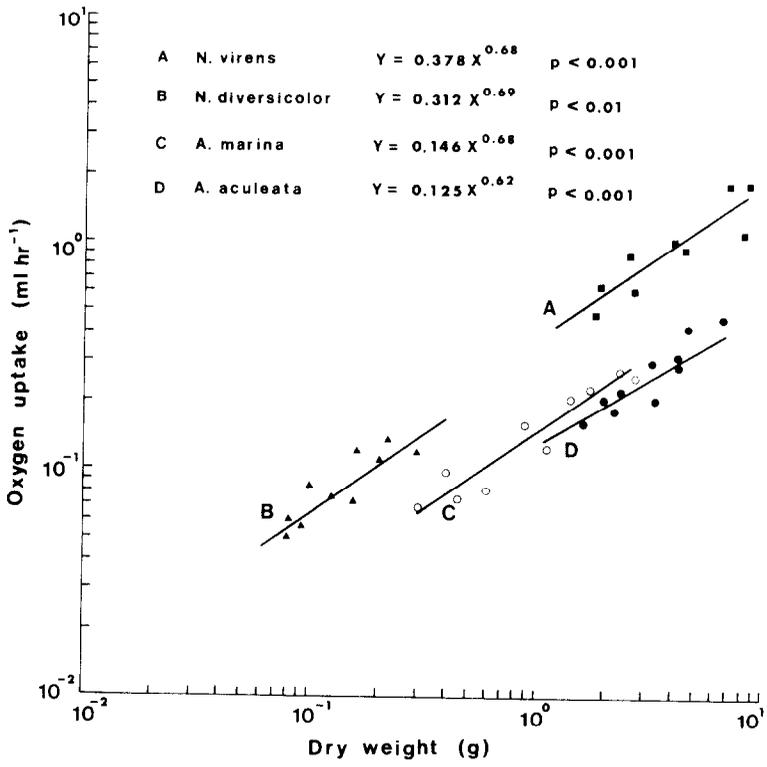


Fig. 1. Oxygen consumption by four species of British polychaetes.

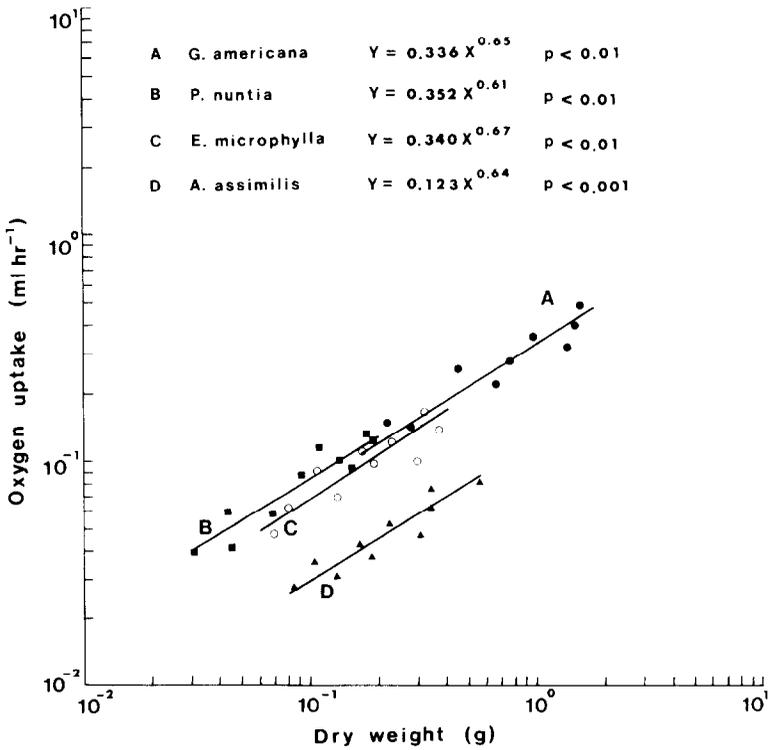


Fig. 2. Oxygen consumption by four species of New Zealand polychaetes.

Table 1. Some relationships between the rate of oxygen consumption and body weight in polychaetes

Species	Range of dry flesh weight (g)	Temp. (°C)	Number of observations (n)	a	b	b'	Authority
<i>Abarenicola assimilis</i>	0.08–0.58	10	10	0.123	0.64	–0.36	This study
<i>Aphrodite aculeata</i>	1.16–6.51	10	10	0.125	0.62	–0.38	This study
<i>Arenicola marina</i>	0.36–1.42*	10–12	6	0.190	0.79	–0.21	Bordon (1931)
<i>Arenicola marina</i>	0.31–2.72	10	9	0.146	0.68	–0.32	This study
<i>Clymenella torquata</i>	0.0015–0.045†	23.5	21		0.48	–0.52	Mangum (1963)
<i>Diopatra cuprea</i>	0.092–0.442†	17.5	17		0.72	–0.28	Mangum & Sassaman (1969)
<i>Eulalia microphylla</i>	0.06–0.41	10	10	0.340	0.67	–0.33	This study
<i>Eupolyornia heterobranchia</i>	0.12–1.12	12–13	37	0.306	0.62	–0.38	Dales (1961a)
<i>Glycera americana</i>	0.16–1.8	10	9	0.336	0.65	–0.35	This study
<i>Glycera dibranchiata</i>		10			0.53	–0.47	Coyer & Mangum (1973)
<i>Hermodice carunculata</i>	0.72–3.0†	26	46	0.510	0.41	–0.59	Sander (1973)
<i>Neoamphitrite robusta</i>	0.61–2.81	12–13	17	0.175	0.43	–0.57	Dales (1961a)
<i>Nereis diversicolor</i>	0.065–0.38	10	10	0.312	0.69	–0.31	This study
<i>Nereis virens</i>	1.18–8.52	10	9	0.378	0.68	–0.32	This study
<i>Perenereis nuntia</i>	0.03–0.20	10	10	0.352	0.61	–0.39	This study
<i>Sabellastarte magnifica</i>	0.72–3.0†	26	50	0.620	0.54	–0.46	Sander (1973)
<i>Schizobranchia insignis</i>	0.08–1.04†	12–13	34	0.051	0.41	–0.59	Dales (1961b)
<i>Thelepus crispus</i>	0.27–1.56	12–13	22	0.209	0.74	–0.26	Dales (1961a)

a and b are fitted parameters in the equation $Y = aX^b$; $b' = b - 1$.

Units are ml $O_2 \cdot hr^{-1}$ (Y) and g dry flesh weight (X).

* Assuming a tissue water content of 85%.

† Assuming a tissue water content of 80%.

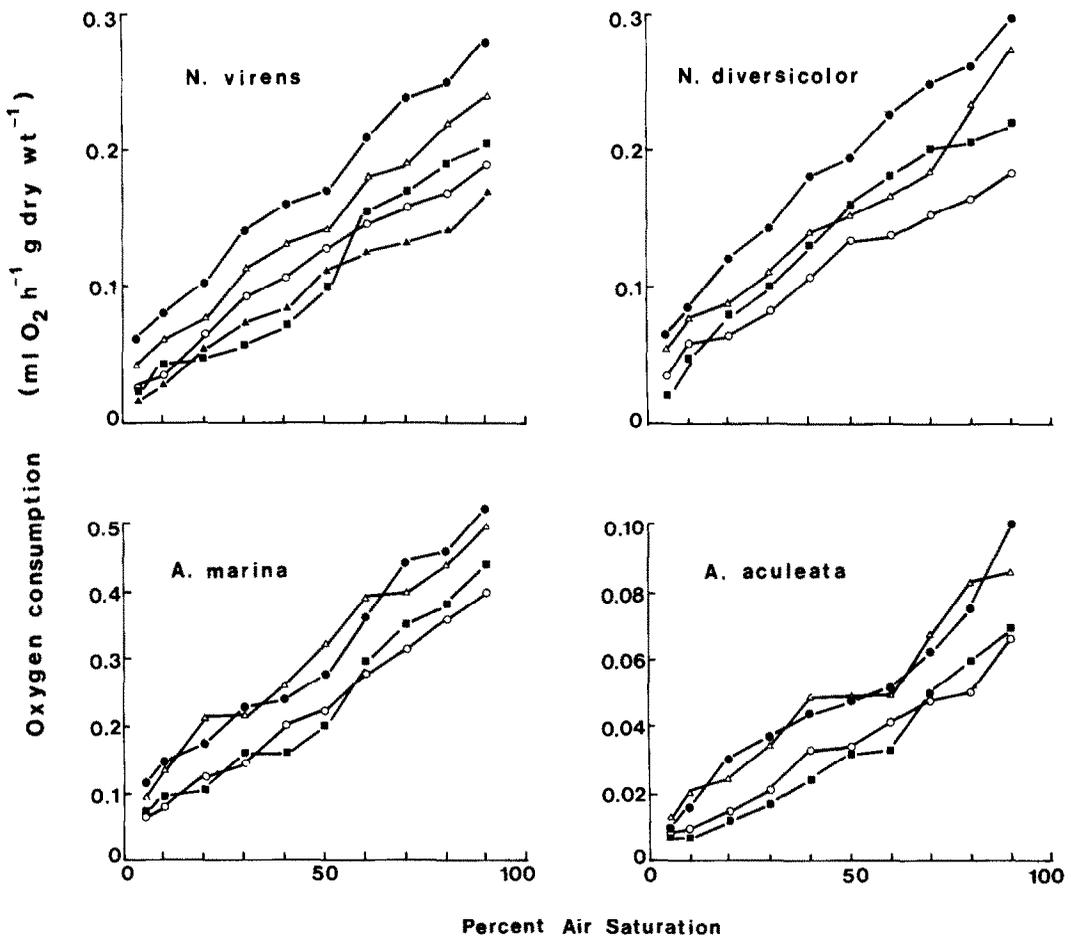


Fig. 3. Oxygen consumption by four species of British polychaetes in declining oxygen tension.

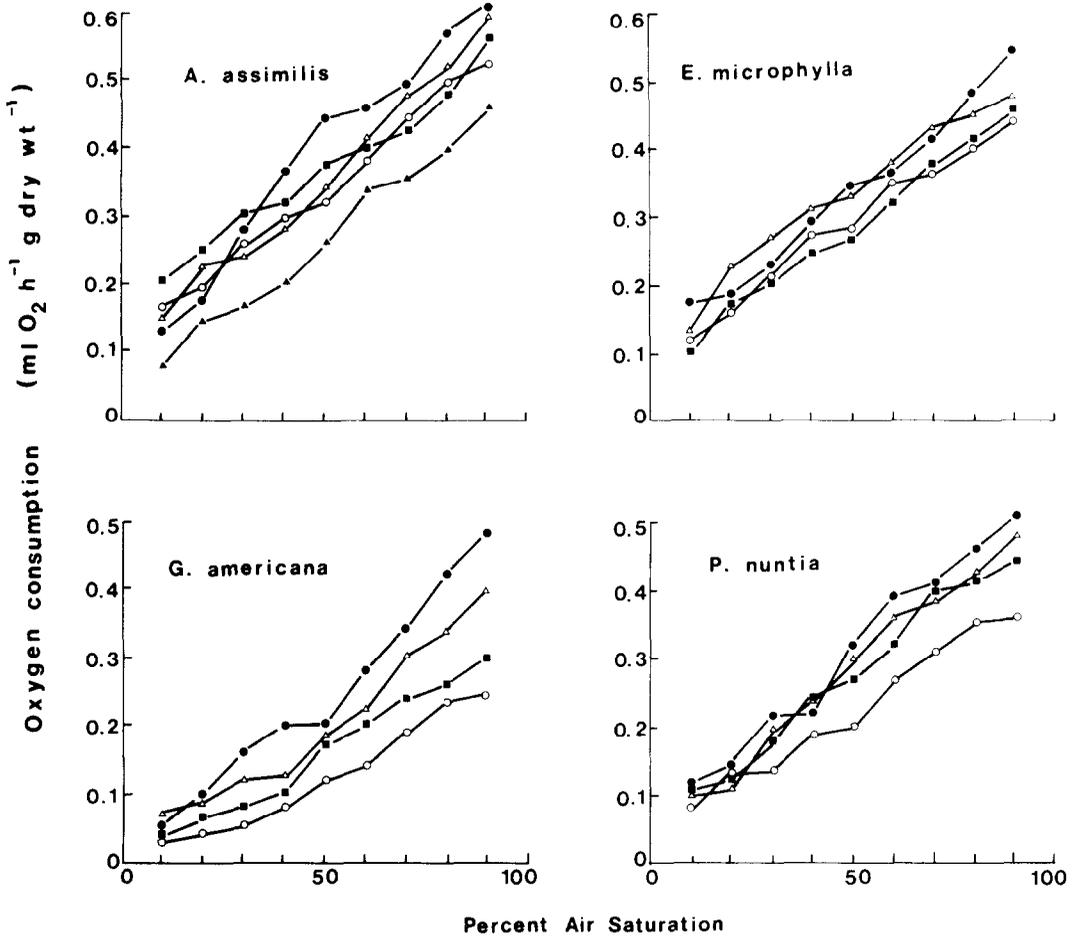


Fig. 4. Oxygen consumption by four species of New Zealand polychaetes in declining oxygen tension.

b is "about 0.75" for poikilothermic animals larger than 1 mg and homeothermic animals. Bertalanffy (1951, 1957) proposed three metabolic types corresponding to different growth types: (1) metabolism is surface proportional, $b = 0.67$; (2) metabolism is weight proportional, $b = 1$; (3) metabolism is intermediate between surface and weight proportionality, $0.67 < b < 1$. As previously pointed out by Hemmingsen (1960) there are many exceptions to Bertalanffy's proposed metabolic types and there is not enough evidence to support these theories. Hemmingsen presents strong evidence for standard metabolism being proportional to the 0.75 power of body weight for all poikilotherms and homeotherms. Hemmingsen's value of 0.75 is based on organisms ranging in size from 10^{-12} to 10^6 grams and in effect represents an average value. Values for the exponent b in polychaetes lie in the range 0.41–0.79 (see Table 1). The simple arithmetic mean of the b values in Table 1 is 0.61 ± 0.11 SD. This value is not significantly different from Hemmingsen's value of 0.75. As Hemmingsen pointed out (1960) b as measured within short weight ranges is not a species specific characteristic and may be affected by state of nutrition, temperature, season or "quite unknown reasons". The wide range of reported b values for polychaetes is probably

accounted for, at least in part, by non-uniform experimental conditions.

Effect of declining PO_2

Animals may be grouped into two classes with respect to the effect of oxygen tension on oxygen consumption (Prosser, 1973). Species in which uptake declines linearly with declining oxygen tension are termed "conformers" (oxygen-dependent) and those in which oxygen uptake remains constant regardless of external oxygen tension are termed "regulators" (oxygen-independent). Dales (1961b) reported that *Schizobranchia insignis* could maintain its normal rate of oxygen consumption down to an external concentration of $2 \text{ cm}^3 \cdot \text{l}^{-1}$ while partial regulation was found in *Hyalinoecia tubicola* (Dales *et al.*, 1970). The majority of reported cases show almost total conformity. Amberson *et al.* (1924–25) found *Nereis virens* to be oxygen-dependent from 760 mm to 76 mm Hg; however, Hyman (1929) maintained that whereas under laboratory conditions oxygen consumption in *N. virens* is dependent upon the external oxygen concentration, when enclosed in tubes oxygen uptake is independent of the external tension. *Abarenicola pacifica* (May, 1972), *Glycera dibranchiata* (Mangum, 1970) and *Sabella pavonina* (Ewer & Fox, 1940) have

Table 2.

Species	Habitat	Authority	'a'
<i>Abarenicola assimilis</i>	Sand & mud burrower; deposit feeder	Morton & Miller (1968)	0.123
<i>Aphrodita aculeata</i>	Sublittoral mud & sand; 'movements rather slow'	Fordham (1925)	0.125
<i>Arenicola marina</i>	Sand & mud flats; permanent burrow; deposit feeder	Green (1968)	0.190 0.146
<i>Hermodice corunculata</i>	'Sluggish in nature'	Sander (1973)	0.115*
<i>Neoamphitrite robusta</i>	Tube dweller; deposit feeder	Ricketts & Calvin (1948)	0.175
<i>Sabellastrata magnifica</i>	Tube dweller; deposit feeder	Sander (1973)	0.161*
<i>Schizobranhia insignis</i>	Tube dweller; deposit feeder	Dales (1961b)	0.051
<i>Thelepus crispus</i>	Tube dweller; deposit feeder	Ricketts & Calvin (1948)	0.209
<i>Eulalia microphylla</i>	Narrow crevices in rocky shores	Morton & Miller (1968)	0.340
<i>Glycera americana</i>	Soft sand and mud; carnivore	Morton & Miller (1968)	0.336
<i>Nereis diversicolor</i>	Estuarine sand & mud; scavenger/ carnivore	Green (1968)	0.312
<i>Nereis virens</i>	Sand & firm mud; predator	Ricketts & Calvin (1948)	0.378
<i>Perenereis nuntia</i>	Sand & mud; carnivore	Morton & Miller (1968)	0.352

'a' is the proportionality constant in the equation $Y = aX^b$; values taken from Table 1.

* Values corrected to 10°C assuming a Q_{10} of 2.5.

all been shown to be oxyconformers. Oxygen consumption by all species in this study was found to be dependent on the external oxygen tension; however, it is probably significant that in the only studies where oxyregulation was reported (Dales, 1961b; Hyman, 1929; Dales *et al.*, 1970) the worms were in artificial burrows which represent a more nearly normal situation for the animals. Further evidence is needed before any generalizations can be made.

Metabolic rate and way of life

In the equation $Y = aX^b$, a is the magnitude of Y when $X = 1$ and therefore provides a comparison of oxygen uptake for different animals of the same weight. Table 2 shows a values and habitats for 13 species of marine polychaetes at similar temperatures (10–12°C). With the exception of two species of sea mice, *Aphrodite aculeata* and *Hermodice corunculata*, the errant and sedentary polychaetes fall into two distinct groups with respect to metabolic rate. The errant polychaetes have a mean a value of 0.344 ± 0.024 while sedentary polychaetes have a mean a value of 0.144 ± 0.047 . Thus, the mean metabolic rate for errant polychaetes (excluding the Aphroditidae) is 2.4 times as high as the rate for sedentary polychaetes. *Aphrodite aculeata* and *Hermodice corunculata* are both known to be very sluggish in nature (Fordham, 1925; Sander, 1973) so it is not surprising that these species, although taxonomically grouped with the errant polychaetes, have metabolic rates similar to the sedentary and tube-dwelling worms.

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