University of Pretoria

Energy system contribution to 2000 m rowing ergometry using the accumulated oxygen deficit

by

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Submitted in partial fulfilment of the requirements for the degree

Magister Scientiae in Human Physiology

in the

Department of Physiology, School of Medicine
Faculty of Health Sciences
University of Pretoria

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2015

ACKNOWLEDGEMENTS

The following individuals are gratefully acknowledged for their invaluable contributions to this research project and/or the completion of this dissertation:

Prof PJ du Toit, Department Physiology, University of Pretoria: for his motivation and patience in supervising this study.

Prof PE Krüger, Director: Institute for Sport Research, University of Pretoria: for his generous support of scientific immersion in the Rowing South Africa national programme and for volunteering the use of the facilities and equipment involved in this study.

Mrs JH Owen, Department of Statistics, University of Pretoria: for her advice and assistance with the data analysis in this study.

Ms L Rademeyer, Assistant Sport Scientist within the Rowing South Africa national programme: for her thorough and efficient administrative support.

Mr R Barrow, **Mr A Grant**, **Mr P Jackson**, **Mr C Felkel**, and other coaches within the Rowing South Africa national programme: for their insight, inquiry and advice on all things rowing.

Dr D Lincoln, **Ms N Macleod**, **Mr G Bruni** and **Dr M Human**, friends and colleagues in the medical and scientific support team of the Rowing South Africa national programme: for their company and advice in uncharted waters.

Rowers in the Rowing South Africa national programme—past, present and undoubtedly in the future: for their willingness to participate in scientific research and their inspirational example.

Friends and colleagues in the Division Biokinetics & Sport Science, Institute for Sport Research, and High Performance Centre, University of Pretoria, past and present: for their enriching and stimulating engagement over many years.

Esmé, Stuart and Bronwyn: for their humour, their sacrifice and their love.

Francé: for making it all worthwhile for a long, long time.

SCIENTIFIC OUTPUTS

Peer-reviewed publications

Clark JR, du Toit PJ. Energy system contribution to 2000 m rowing ergometry. [In preparation].

Congress presentations

Clark JR. Energy system contribution to 2000 m rowing ergometry. **Annual Congress of South African Academy for Science and Arts, Division Biological Sciences**, Pretoria, 16 October 2013. [Oral presentation].

Clark JR. Energy system contribution to 2000 m rowing ergometry. **Physiology Society of Southern Africa Annual Congress**, Pretoria, 15-18 September 2013. [Oral presentation].

Clark JR. Energy system contribution and correlates to performance in a 2000 m rowing ergometry time trial in South African rowers. **University of Pretoria Health Sciences Faculty Research Day**, Pretoria, 20-21 August 2013. [Poster presentation].

Clark JR. Energy system contribution and correlates of performance to a 2000 m rowing ergometry time trial in South African Rowers. **British Association of Sport and Exercise Sciences Student Conference**, London, 11-12 April 2012. [Oral presentation].

Clark JR. Energy system contribution to 2000 m rowing ergometry. **Physiology Society of Southern Africa Annual Congress**, Pretoria, 16-19 September 2008. [Oral presentation].

Clark JR. Energy system contribution to 2000 m rowing ergometry. **International Sports Medicine Congress of the South African Sports Medicine Association**, Pretoria, 14-16 November 2007. [Poster presentation].

Clark JR. Energy system contribution to 2000 m rowing ergometry. **Physiology Society of Southern Africa Annual Congress**, Cradle of Humankind, 9-12 September 2007. [Poster presentation].

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ADP	adenosine diphosphate
AMP	adenosine monophosphate
AOD	accumulated oxygen deficit
ATP	adenosine triphosphate
ATPase	adenosine triphosphatase
b	beats
^{13}C	carbon-13
Ca^{2+}	calcium ion
CI	confidence interval
CK	creatine kinase
cm	centimetre
CO	cytochrome oxidase
CO_2	carbon dioxide
CoA	coenzyme A
Cr	creatine
CS	citrate synthase
dm	dry mass
e.g.	for example
EPOC	excess post-exercise oxygen consumption
eq	equivalent
et al.	and others
ETC	electron transfer chain
FAD	flavin adenine dinucleotide, oxidized
$FADH_2$	flavin adenine dinucleotide, reduced
GAPDH	glyceraldehyde 3-phosphate dehydrogenase
^1H	hydrogen-1
H^+	hydrogen ion
H_2O	water
Hg	mercury
HK	hexokinase
HR	heart rate
HR_{max}	maximum heart rate
HR_{peak}	peak heart rate
HSL	hormone-sensitive lipase
IDH	isocitrate dehydrogenase
IMP	inosine monophosphate
ISAK	International Society for the Advancement of Kinanthropometry
K^+	potassium ion
KDH	alpha-ketoglutarate dehydrogenase
kg	kilogram
kJ	kilojoule
L	litre
LDH	lactate dehydrogenase
LPL	lipoprotein lipase
m	metre
min	minute
ml	millilitre
mm	millimetre
mmol	millimole
MRI	magnetic resonance imaging
n	number of participants in the sample
Na^+	sodium ion
NAD^+	nicotinamide adenine dinucleotide, oxidized
NADH	nicotinamide adenine dinucleotide, reduced

nmol	nanomole
O_2	oxygen
P	level of significance
^{31}P	phosphorous-31
PBT	personal best time
PC	phosphocreatine
PDH	pyruvate dehydrogenase
PFK	phosphofructokinase
pH	relative acidity or alkalinity
PHOS	phosphorylase
P_i	inorganic phosphate
PK	pyruvate kinase
PO	power output
r	correlation coefficient
R^2	square of interclass correlation coefficient, common variance
RH	relative humidity
rho	Spearman’s rank order correlation coefficient
s	second
SD	standard deviation
SEE	standard error of estimate
SR	sarcoplasmic reticulum
STPD	standard temperature, pressure, dry
TCA	tricarboxylic acid
UK	United Kingdom
USA	United States of America
VCO_2	pulmonary carbon dioxide elimination
VO_2	pulmonary oxygen uptake
VO_{2max}	maximum oxygen uptake
VO_{2peak}	peak oxygen uptake
W	watt
%	percent
°C	degrees Celsius
≈	approximately equals
=	equals
±	plus-minus
<	less than
>	greater than
/	or

ABSTRACT

Title:	Energy system contribution to 2000 m rowing ergometry using the accumulated oxygen deficit
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Exercise scientists and coaches frequently base physical conditioning objectives on the nature and magnitude of the physiological demands imposed by competitive events. Part of this demand may be characterized by the extent and proportion of aerobic and anaerobic energy supply associated with performing an athletic task. Maximum effort rowing imposes severe physiological demands owing to high force application per stroke, extensive skeletal muscle involvement, and repetition of a unique movement pattern, distinguishing it somewhat from other endurance exercise modalities. Rowing ergometry represents a valid and reliable simulation of the biomechanical and physiological demands of on-water rowing, and the 2000 m rowing ergometer time trial has become a standard physical performance test for rowers. However, empirical information regarding proportional aerobic and anaerobic energy supply during maximum effort 2000 m rowing is scarce. Studies which have investigated the theme report a proportional dominance (70-90%) by aerobic energy supply, but the research studies are limited in number and dissimilar in methodology. Further, models of relative energy system contribution popularized in traditional textbooks frequently do not mirror the results of these studies. The accumulated oxygen (O_2) deficit (AOD) method, despite limitations, remains a preferred method for differentiating aerobic and anaerobic energy supply during dynamic, whole-body exercise in athletes, yet few AOD measurements have been made on rowers during 2000 m rowing ergometer time trials. Also, while several anthropometric and physiological characteristics have long been shown to be associated with rowing performance, relationships between energy system contributions and performance do not appear to have been investigated to date. The purpose of this study was to quantify the relative energy system contributions during a maximum effort 2000 m rowing ergometer time trial, and to determine the correlations between performance and measures of aerobic and anaerobic energy supply.

A quantitative, cross-sectional research study was designed to obtain descriptive and correlational data from a sample of elite oarsmen during a single observation period. Twenty-five national and international level male rowers (mean ± standard deviation [SD] age: 21.0 ± 3.6 years, rowing training history: 5.7 ± 3.4 years, maximum O_2 uptake [VO_{2max}]: 4.64 ± 0.54 $L{\cdot}min^{-1}$ or 58.9 ± 5.3 $ml{\cdot}kg^{-1}{\cdot}min^{-1}$) from the South African national rowing squad volunteered as participants. In the first of two separate test sessions within a period spanning no more than five days, participants underwent anthropometric assessment (body mass: 78.9 ± 7.6 kg, stature: 185.2 ± 5.5 cm, sum-of-seven skinfolds: 53.6 ± 9.8 mm) and completed a 2000 m time trial (performance time: 405.6 ± 20.5 s, range: 373.0-452.0 s) on a Concept II rowing ergometer. The second session involved an incremental rowing ergometer exercise test including five or six submaximal intensity stages spanning the range 35-85% of time trial average power output, and a maximum effort stage to determine peak power output and VO_{2max}. Pulmonary O_2 uptake (VO_2) was recorded continuously during exercise via open-circuit spirometry. Aerobic energy supply was determined from accumulated O_2 uptake during the time trial, while anaerobic energy supply was calculated from the AOD. Specifically, incremental exercise test data was used to establish the VO_2-power output relationship (R^2: 0.995 ± 0.004, SEE: 0.061 ± 0.028 $L{\cdot}min^{-1}$) for each participant, which was solved for average power output to yield the total equivalent O_2 demand of the 2000 m time trial. The difference between accumulated O_2 uptake and total equivalent O_2 demand represented the AOD. Descriptive statistics were used to report physiological responses and measures of aerobic and anaerobic energy supply, while Spearman rank order correlation coefficients (rho) were calculated to evaluate the relationships between energy system measures and 2000 m time trial performance.

The principal finding of this study was—in agreement with earlier research reports—that aerobic and anaerobic energy supply respectively represented 80-82% (range: 73-93%) and 18-20% (range: 7-27%) of total energy cost during a maximum effort 2000 m rowing ergometer time trial. Notably, relative energy system contribution showed considerable variation among participants which could not be fully explained by differences in exercise duration, since the correlations between time trial performance and energy system fractional contributions, while significant ($P < 0.05$), were not strong (rho: 0.5-0.6). While significant relationships were also found between 2000 m performance time and age, rowing training history, body mass, stature, accumulated O_2 uptake and AOD, only VO_{2max} and peak VO_2 (VO_{2peak}) expressed in absolute terms, peak power output, and total equivalent O_2 demand demonstrated strong (rho: 0.82-0.96) correlations with 2000 m rowing ergometer performance time.

Aerobic energy supply dominates total energy provision during a maximum effort 2000 m rowing ergometer time trial, with VO_2 reaching rates exceeding 97% of VO_{2max}. However, AOD values recorded in this study (6.10 L O_2 eq or 76.9 ml O_2 $eq \cdot kg^{-1}$) support the argument that 2000 m rowing involves extensive utilization of anaerobic capacity. So while aerobic energy supply dominates proportionally, the absolute values of aerobic and anaerobic energy supply reported here underscore the large cumulative energy demand imposed by a 2000 m rowing ergometer time trial. Significant relationships commonly observed between rowing performance and rower characteristics, including measures of body size and endurance fitness, were corroborated by this study. However, the ability to produce and sustain a high power output during rowing, necessarily supported by the capacity for high absolute rates of both aerobic and anaerobic energy supply—regardless of their respective contributions—was the bioenergetic capability most strongly related to performance in a 2000 m rowing ergometer time trial in this study.

Improved understanding of aerobic and anaerobic energy supply during simulated rowing races such as the 2000 m rowing ergometer time trial has practical utility for exercise scientists and coaches in terms of rower identification and management, as well as in the planning, regulating and monitoring of rowing training programmes. Future investigations should consider assessing seasonal changes in the relative energy system contributions for a 2000 m rowing ergometer time trial, and distribution of aerobic and anaerobic energy supply in relation to the regulation of power output (pacing) during simulated rowing races.

Key words: rowing, aerobic and anaerobic energy supply, accumulated oxygen deficit, performance.

ABSTRAK

Titel:	Energiestelselbydrae tot 2000 m roei-ergometrie deur middel van die opgehoopte suurstoftekort
Kandidaat:	Mnr JR Clark
Promotor:	Prof PJ du Toit
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Sportwetenskaplikes en -afrigters baseer gereeld fisiese kondisioneeringsdoelwitte op die aard en omvang van die fisiologiese eise wat deur die betrokke sport items gestel word. ‘n Gedeelte van hierdie eise kan voorgestel word deur die betrokke omvang en proporsie van aerobiese- en anaerobiese energievoorsiening. Maksimum-roeiprestasie stel streng fisiologiese eise as gevolg van hoë kraguitset tydens die beweging, uitgebreide betrokkenheid van die skeletspiere, en die herhaling van 'n unieke bewegingspatroon, wat dit onderskei van ander uithouvermoë oefeningsmodaliteite. Roei-ergometrie verteenwoordig 'n geldige en betroubare simulasie van die biomeganiese- en fisiologiese eise van roei op water, en die 2000 m roei-ergometer tydtoets het 'n standaard fisiese prestasietoets vir roeiers geword. Empiriese inligting oor proporsionele aerobiese- en anaerobiese energievoorsiening tydens ‘n maksimum-poging 2000 m roei-item is egter skaars. Studies wat die tema al ondersoek het dui op ‘n oorheersend aerobiese energievoorsiening (70-90%), maar die navorsing is beperk in hoeveelheid en uiteenlopend in metodiek. Verder weerspieël modelle wat die relatiewe bydraes van energiestelsels in populêre handboeke aandui dikwels nie die resultate van hierdie studies nie. Die opgehoopte suurstof (O_2) tekort (AOD) metode bly, ten spyte van beperkings, 'n gewilde wyse om tussen aerobiese- en anaerobiese energievoorsiening tydens dinamiese, hele liggaam oefening in atlete te onderskei. Ten spyte hiervan is daar nog min AOD metings tydens 2000 m roei-ergometer tydtoets op roeiers gerapporteer. Verder, alhoewel verskeie antropometriese- en fisiologiese eienskappe lank reeds bewys is om verband te hou met roeiprestasie, is verhoudings tussen energiestelselbydraes en roeiprestasie klaarblyklik tot op datum nog nie ondersoek nie. Die doel van hierdie studie was om die relatiewe energiestelselbydraes tydens 'n maksimum-poging 2000 m roei-ergometer tydtoets te kwantifiseer, en om korrelasies tussen prestasie en maatstawwe van aerobiese- en anaerobiese energievoorsiening te bepaal.

'n Kwantitatiewe, deursnewende navorsingstudie is uitgevoer om beskrywende- en korrelasiedata van 'n groep elite roeiers tydens 'n enkele evalueringsperiode te verkry. Vyf-en-twintig nasionale- en internasionale vlak manlike roeiers (gemiddeld ± standaardafwyking [SD] ouderdom: 21.0 ± 3.6 jaar, roei inoefeningsgeskiedenis: 5.7 ± 3.4 jaar, maksimale O_2 opname [VO_{2maks}]: 4.64 ± 0.54 $L \cdot min^{-1}$ of 58.9 ± 5.3 $ml \cdot kg^{-1} \cdot min^{-1}$) van die Suid-Afrikaanse nasionale roeispan het vrywillig aan die studie deelgeneem. In die eerste van twee afsonderlike evalueringsessies, wat nie meer as vyf dae uitmekaar plaasgevind het nie, het deelnemers antropometriese assessering ondergaan (liggaamsmassa: 78.9 ± 7.6 kg, liggaamslengte: 185.2 ± 5.5 cm, som-van-sewe velvoue: 53.6 ± 9.8 mm) en 'n 2000 m tydtoets (tyd: 405.6 ± 20.5 s, reikwydte: 373.0-452.0 s) op 'n Concept II roei-ergometer afgelê. Die tweede evalueringsessie het 'n inkrementele roei-ergometer oefentoets behels, insluitend vyf of ses submaksimale intensiteitsfases met die reikwydte 35-85% van gemiddelde kraguitset tydens die tydtoets, en 'n maksimum-poging fase om piek kraguitset en VO_{2maks} te bepaal. Pulmonale O_2 opname (VO_2) is voortdurend tydens oefening aangeteken via oop-kring spirometrie. Aerobiese energievoorsiening is deur middel van die opgehoopte O_2 opname tydens die tydtoets bepaal terwyl anaerobiese energievoorsiening deur middel van die AOD bereken is. Meer spesifiek is inkrementele oefentoetsdata gebruik om 'n VO_2-kraguitset verhouding (R^2: 0.995 ± 0.004, SEE: 0.061 ± 0.028 $L \cdot min^{-1}$) vir elke deelnemer vir gemiddelde kraguitset op te los om die totale ekwivalente O_2 aanvraag van die tydtoets te bepaal. Die verskil tussen opgehoopte O_2 opname en totale ekwivalent O_2 aanvraag verteenwoordig die AOD. Beskrywende statistiek is gebruik om fisiologiese response en maatstawwe van aerobiese- en anaerobiese energievoorsiening te rapporteer, terwyl Spearman rangorde korrelasiekoëffisiënte (rho) bereken is om die verhouding tussen energiestelsel maatstawwe en 2000 m tydtoetsprestasie te evalueer.

Die hoof bevinding van hierdie studie was—in ooreenstemming met vorige navorsingsverslae—dat aerobiese en anaerobiese energiebydraes onderskeidelik 80-82% (reikwydte: 73-93%) en 18-20% (reikwydte: 7-27%) van die totale energiebehoefte tydens 'n maksimum-poging 2000 m roei-ergometer tydtoets verteenwoordig. Relatiewe energiestelselbydrae het aansienlike variasie tussen deelnemers getoon wat nie ten volle deur verskille in oefeningsduur verklaar kan word nie, aangesien die korrelasie tussen tydtoetsprestasie en energiestelsel fraksionele bydraes beduident ($P < 0.05$) maar nie sterk (rho: 0.5-0.6) was nie. Terwyl beduidende verhoudings ook tussen 2000 m prestasietyd en ouderdom, roei inoefeningsgeskiedenis, liggaamsmassa, liggaamslengte, opgehoopte O_2 opname en AOD gevind is, het net VO_{2maks} en piek VO_2 (VO_{2piek}) uitgedruk in absolute terme, piek kraguitset, en totale ekwivalente O_2 aanvraag sterk (rho: 0.82-0.96) korrelasies met 2000 m roei-ergometer prestasietyd getoon.

Aerobiese energievoorsiening oorheers totale energievoorsiening tydens 'n maksimum-poging 2000 m roei-ergometer tydtoets, met VO_2 wat meer as 97% van VO_{2maks} bereik. Terselfdertyd is AOD waardes (6.10 L O_2 ek of 76.9 ml O_2 ek·kg^{-1}) in hierdie studie onder die hoogste gerapporteer in gepubliseerde literatuur, wat die argument dat 2000 m roei uitgebreide gebruik van die anaerobiese energiekapasiteit behels, ondersteun. Terwyl aerobiese energievoorsiening proporsioneel oorheers, beklemtoon die absolute waardes van aerobiese- en anaerobiese energievoorsiening aangeteken in hierdie studie die groot kumulatiewe aanvraag na energie tydens 'n 2000 m roei-ergometer tydtoets. Betekenisvolle verbande wat algemeen waargeneem word tussen roeiprestasie en roeier eienskappe, insluitend maatstawwe van liggaamsgrootte en uithouvermoëfiksheid, is in hierdie studie bevestig. Maar, die vermoë om 'n hoë kraguitset tydens roei te produseer en te handhaaf, wat noodwendig deur ‘n kapasiteit vir hoë absolute aerobiese- en anaerobiese energievoorsiening ondersteun word—ongeag hul onderskeie bydraes—is die bioenergetiese vermoë wat die sterkste verband hou met prestasie in 'n 2000 m roei-ergometer tydtoets.

‘n Beter begrip van aerobiese- en anaerobiese energievoorsiening tydens gesimuleerde roei-items soos die 2000 m roei-ergometer tydtoets het praktiese nut vir oefenwetenskaplikes en afrigters in terme van identifikasie en bestuur van roeiers, asook in die beplanning, regulering en monitering van roei oefenprogramme. Verdere navorsing wat oorweeg moet word sluit in die invloed van seisoenale veranderings op relatiewe energiestelselbydraes tydens 'n 2000 m roei-ergometer tydtoets, en die verspreiding van aerobiese- en anaerobiese energievoorsiening in vergelyking met die regulering van kraguitset tydens gesimuleerde roei-items.

Sleutelwoorde: roei, aerobiese- en anaerobiese energievoorsiening, opgehoopte suurstof tekort, prestasie.

CHAPTER 1

INTRODUCTION

1.1 Background and Rationale

Scientific research into performance, preparation and prediction in sport continues to advance in attempt to explain, reproduce and ultimately improve competitive performance [1]. Among the myriad themes characterising scientific inquiry in sport, describing the demands of competitive events and elucidating athlete characteristics linked to successful performance have fundamental practical utility in the design of effective interventions aimed at improving performance [2]. Assessing the acute responses of athletes during exercise permits the nature and magnitude of the demands imposed by an exercise task to be quantified—the responses being largely a function of athlete genotype, training status and the nature of the exercise task [3]. Measuring athlete responses during exercise may therefore aid in understanding physical fitness requirements, characterizing responses associated with superior performance, and directing athlete identification and preparation for athletic events—collectively known as modelling elite sport performance [4]. Appropriate use of exercise testing in sport programmes may thus elevate enhanced competitive performance to the realm of planned process rather than chance occurrence [5].

Describing the physiological responses to exercise is by no means a novel concept [6]. The most relevant expressions of the physiological demands of athletic performance are recorded when experienced athletes are assessed while performing maximum effort, sport-specific exercise tasks, ideally within the competitive environment [5]. Since the last mentioned condition is often neither possible nor desirable, simulated performance trials which replicate competitive demands represent the best alternative [3]. Constant work tests, also known as time trials, require the completion of a set amount of distance as quickly as possible and according to Hopkins *et al*. [7] "*…represent good simulations of the bioenergetics of most competitive events lasting several minutes or more.*" Other test formats such as all-out effort or constant power output exercise may well provide information about physical capacity but not elicit performance-specific responses nor elucidate the nature of their regulation and integration [8]. Exercise test criteria which appear essential in appropriately profiling the physiological demands of a sport include the performance of self-paced, maximum effort, event-specific exercise tasks by athletes of a high calibre [9]. Failure to adequately simulate the requirements of an athletic event renders the practical value of measuring the physiological demands of a sport low [3].

Rowing involves intense, dynamic, whole-body exercise requiring considerable endurance, strength and technical skill [10], and has attracted scientific inquiry since the pioneering era of investigations into human exercise performance [11]. Its scientific appeal may lie in its considerable demands: competitive rowing represents a challenge to several physiological capacities and a profound test of integrative regulation of homeostasis during exercise [12]. Since ergometer rowing represents a valid and reliable simulation of the biomechanical and physiological demands of on-water rowing [13], ergometer exercise performance is commonly used as a measure of rowing-specific physical and physiological capacity [14]. The simulated 2000 m rowing ergometer time trial has become a standard physical performance test for rowing [4].

Bangsbo [15] suggested that exercise physiologists have been captivated by the involvement of energy supply systems in support of muscular exercise since the mechanisms of adenosine triphosphate (ATP) regeneration were elucidated. The sentiment appears supported judging by the attention the theme enjoys in many contemporary texts supporting courses in exercise physiology [16-19]. The biochemistry of energy supply mechanisms in skeletal muscle has been extensively researched *in vitro* to yield detailed descriptions of the substrates, regulation and interactions of aerobic and anaerobic processes involved in protecting the energy state of the cell [20-22]. Several methods, each with benefits and limitations, have been used in attempts to evaluate the involvement and relative contribution of these energy supply mechanisms during exercise [9, 23]. While modern apparatus for measuring pulmonary oxygen uptake (VO_2) provide sufficient precision to indicate aerobic energy yield [24, 25], no universally accepted method exists for quantifying anaerobic energy supply and many concerns exist regarding the techniques that have been employed [9]. Despite criticism [15], the accumulated oxygen deficit (AOD) method has been the most popular technique and has previously [26] and more recently [27] been suggested as a preferred means of appropriately differentiating between aerobic and anaerobic energy yield during intense, dynamic, whole-body exercise in athletes. However, while recommended to practitioners for assessing anaerobic capacity in rowers, Hahn *et al*. [28] pointed out that few AOD measurements have been made on rowers using the 2000 m ergometer test.

An examination of the scientific literature reveals that a limited number of studies have investigated the relative contribution of energy supply systems during a simulated rowing event.

In the earliest of these investigations [29-32], methodological concerns regarding exercise format, ergometer design and assessment technique raise doubt over the applicability of the results. Yet some contemporary texts used by rowing coaches [33, 34] still relay these initial, potentially erroneous estimations of the energy system contributions in rowing. In the studies that made use of the AOD method during rowing [29, 32, 35-37] the reportage of net versus gross energy demand and consideration of peripheral oxygen (O_2) store utilization is generally inconsistent. In short, while studies investigating energy system involvement during maximum effort rowing simulations all report a predominance of aerobic energy supply, results vary fairly widely from 70% to 90% of total energy demand, the studies are limited in number, and have employed disparate methodologies [29, 32, 35-37].

Despite inconsistencies in individual study methodology, collectively the results of studies on the energy system contributions during rowing differ markedly from the estimates provided in some widely popularized models on the theme, which propose a lower reliance on aerobic energy supply approximating 55% to 60% of total energy demand [16, 19]. These texts may have reproduced and popularized the results of early studies which estimated aerobic and anaerobic energy system contributions during exercise using cycling or running modalities and measurement techniques of questionable validity [38-40]. While competitive performance times are comparable to other intermediate duration endurance sport events, rowing differs fundamentally from other locomotive forms of exercise like cycling or running in the nature and extent of skeletal muscle involvement and the morphology of successful participants [10, 12], factors among those which influence aerobic and anaerobic energy release [26]. Estimating energy system involvement in rowing from the results of studies using other exercise modalities based on similar performance time may therefore be inappropriate.

Many studies have attempted to elucidate factors related to rowing success, and a number of anthropometrical [35, 41-45] and physiological [35, 36, 41, 43, 46-56] characteristics in rowers have consistently been linked with rowing performance. Among these are characteristics indicative of the capacity for aerobic and anaerobic energy release, typically measured independently rather than during a rowing time trial. Further, Pripstein *et al*. [36] demonstrated that in rowers, the capacity for anaerobic energy supply was significantly related to measures of aerobic energy capacity, highlighting the interdependence between energy supply mechanisms in meeting the large total energy demand imposed by a rowing event. However, whether rowing performance is related to the relative contributions of the energy supply systems during a performance trial does not appear to have been investigated.

Information regarding the mechanisms of energy supply during exercise and how these relate to performance is of practical importance in understanding sport demands, profiling elite performers and directing athletic preparation. In light of standardized rowing equipment, stabilized selection pressure for individuals of large body size, plateaued increase in training volume and the professional sporting lifestyle of many world-class rowers, Secher & Vogelsang [34] have suggested that further improvement in rowing performance will be a product of better training quality and the development rowers with improved skill. The former almost certainly necessitates that significant value be placed on the identification of individual rower physical profiles, the specific demands of the sport and factors related to rowing performance.

Strydom *et al*. [57] appear to have published the earliest set of data on physiological characteristics of South African rowers when they measured heart rate and VO_2 during treadmill running and rowing. These researchers recognized the potential of science to support elite sporting endeavours and bemoaned the lack of collaboration between physiologists and coaches in the country [57]. Almost fifty years later, immersion of scientific inquiry into rowing in South Africa is largely limited to a single centre [58], and published rowing-specific physiological and performance data from within South Africa remains lacking. The result is a scarcity of locally relevant information for systematic use in current and future athlete profiling, comparison and development. Meaningful scientific contribution to the improvement of the performances of South African rowers through tailored training programmes requires, among other things, thorough understanding of rowing performance demands and close inspection of individual responses to rowing performances.

In summary, a need exists to clarify, challenge or corroborate previous estimates of the aerobic and anaerobic energy supply during a rowing performance. Credibly addressing the concerns outlined above requires the assessment of well-trained rowers during an event-specific performance, an analysis method appropriate for intense, dynamic, whole-body exercise, and explicit presentation of computational permutations. The primary aim of this study was therefore to determine the relative aerobic and anaerobic energy supply contributions to a maximum effort 2000 m rowing ergometer time trial performance in national and international level rowers using the AOD method. A secondary aim was to determine whether significant relationships exist between measures of energy system involvement and rowing ergometer time trial performance.

1.2 Hypotheses

The following research hypotheses were developed congruent with the aims presented above:

- There exists a predominance of aerobic energy supply during a 2000 m rowing ergometer time trial which approximates 80% of the estimated gross energy demand of the performance; and
- Significant correlations exist between performance time and measures of both aerobic and anaerobic energy supply during the 2000 m rowing ergometer time trial.

The first hypothesis is based on the range of results from previous studies which investigated energy system contributions in rowers of various abilities and involved dissimilar techniques and/or considerations [29-32, 35-37, 59]. The second hypothesis is based on several observations from the scientific literature. Firstly, models describing the relative energy system contributions during maximum effort exercise tasks contend that anaerobic energy system contribution is larger when performance time is shorter [16-19, 60]. Secondly, studies have consistently shown that maximum oxygen uptake (VO_{2max}), indicative of the highest attainable rate of aerobic energy supply, is related to 2000 m rowing performance [35, 41, 43, 47, 50-53, 56]. Lastly, the nature and magnitude of force application in rowing has prompted suggestions that a high capacity for anaerobic energy supply is advantageous to rowing performance [41].

1.3 Type of Research

On a continuum between pure and applied scientific inquiry [61], in the context of the information described above, this study represents applied research, undertaken to answer specific questions about energy system contributions during a maximum effort rowing ergometer performance. While the advancement of knowledge and understanding in the theme may be fundamental to this research, the results of this study are applicable to professionals involved in the physical preparation of competitive rowers, and are intended to help guide meaningful rowing training interventions [62]. In other words, the results are of practical significance for the purposeful preparation of rowers for the specific demands of the sport.

This study represents a descriptive investigation of the relative aerobic and anaerobic energy supply contributions during a 2000 m rowing ergometer time trial performance, and of the relationships between the energy supply contributions and rowing ergometer performance. As descriptive and correlational research [62], empirical measurements and analyses of original, quantitative data were used to deductively address the research problems identified above [61]. Further, this study represents primary research in a cross-sectional design, appropriate for the collection and analysis of data to describe existing phenomena and relationships without any intervention or measure to elucidate reasons for the phenomena [62].

1.4 Outline and Scope

Chapter 1 serves as background to this study and introduces pertinent themes and the research framework applicable to this investigation. Chapter 2 reviews literature relevant to the research problem, including the involvement and measurement of aerobic and anaerobic energy supply during exercise and the applied physiology of rowing. Significant attention is given to literature addressing the AOD as a means of quantifying anaerobic energy release during exercise, and to previous investigations of the aerobic and anaerobic energy supply during rowing. The materials and methods employed in this study are outlined in Chapter 3, including sections describing the research participants, exercise test procedures and data handling to obtain the derived measures. The results of this study can be found in Chapter 4, with subsections dedicated to the descriptive and correlation analyses. Chapter 5 contains a discussion of the findings on each parameter against the background of existing data on the theme. Interpreting the results is supplemented with acknowledging important limitations and assumptions inherent in this study and its methods. Finally, Chapter 6 concludes with a summary of the major findings of this study and suggests practical applications and recommendations. References cited in the text are collated by order of citing in a single list at the end of this dissertation, followed by Appendices of relevant documentation used in this study.

CHAPTER 2
LITERATURE REVIEW

2.1 Energy System Contributions during Maximum Effort Exercise

2.1.1 Background

There are significant conceptual and practical implications to understanding the involvement and relative contribution of energy supply mechanisms during an exercise task [9]. For instance, recognition of the nature and extent of demands placed on energy supply during sport-specific exercise tests may help to define minimum benchmarks in physiological capacities for competitive success [63]. Measurement of energy system involvement during maximum effort exercise tasks may assist in the allocation of preparation time or activities for developing event-specific physical fitness [4]. Planned implementation of sport-specific physical training is a fundamental principle in athletic preparation which requires that, among other things, the energy supply demands of a sport are accurately described [63]. These represent important practical concerns for coaches, scientists and conditioning staff involved in implementing preparation plans targeted at improving sport performance.

The first section of this chapter summarizes a contemporary understanding of human skeletal muscle energy supply during exercise. Most attention is given to the interdependence of energy supply processes and energy system involvement and relative contribution during single bouts of maximum effort exercise. For the purposes of this study, maximum effort exercise describes the performance of an exercise task to the best ability of the participant, irrespective of intensity, duration, modality or format [7]. Unless otherwise stated, maximum effort exercise is implied when reference to energy system responses during exercise is made. This section is not dedicated to an exhaustive discussion of skeletal muscle bioenergetics *per se*, but rather to providing a coherent description of energy system response during exercise and the factors influencing this response. Some appreciation of skeletal muscle cell architecture, motor unit excitation-contraction coupling and systemic physiological responses to acute exercise is required, but inclusion of such material would be prohibitively lengthy. Additionally, themes related to the bioenergetics of exercise but which are expressly not included in this section since they exist beyond the scope of the research question include: biochemistry of skeletal muscle contraction; thermodynamics of the energy system chemical reactions; intermediary metabolism and transformation of carbohydrate, lipid and protein derivatives; muscle bioenergetics prior to and following exercise; and the integrative role of energy system substrate and metabolite concentrations in exercise-associated fatigue. Extensive reviews of these themes are available [20-22, 64-68].

2.1.2 Energy Supply Mechanisms in Skeletal Muscle

2.1.2.1 Adenosine Triphosphate

The intracellular mechanical events of skeletal muscle force generation are the result of repeated interactions between actin and myosin proteins within the myofibril complexes [69]. Actomyosin cycling is intimately coupled to the exergonic hydrolysis of adenosine triphosphate (ATP) by myosin adenosine triphosphatase (ATPase), yielding adenosine diphosphate (ADP), inorganic phosphate (P_i) and hydrogen ion (H^+) [70]. The chemical potential energy of ATP, liberated through hydrolysis of its two terminal anhydride bonds, supports the mechanical work of contractile activity [71]. Other processes necessary for skeletal muscle contractile activity which are also reliant on this energy transduction reaction are active transport of calcium ion (Ca^{2+}) across the sarcoplasmic reticulum (SR) membrane and maintenance of the sodium-potassium ion (Na^+-K^+) electrochemical gradient across the sarcolemma [69].

The concentration of ATP in resting skeletal muscle approximates 20 to 25 $mmol \cdot kgdm^{-1}$ [70]. In light of the innumerable myosin, Ca^{2+} and Na^+-K^+ ATPase sites within each fibre of a skeletal muscle, such a store is severely limited in comparison to the capacity for ATP hydrolysis during maximum contractile activity [65]. An ATP utilization rate 500 to 1000 times faster than at rest imposes a profound metabolic burden on active skeletal muscle [67]. While sarcoplasmic ATP represents the immediate ATPase substrate, this store is insufficient to maintain muscle contractile activity beyond approximately 1 to 2 s [22]. Yet useful skeletal muscle force production is only possible through sustained, repeated or extensive contractile activity [60]. This contractile activity largely determines the rate of ATP utilization in skeletal muscle and therefore the demand for its regeneration [67]. For the purposes of this study, energy systems refer to the intracellular chemical processes that attempt to meet this demand [72].

Other biological work processes such as macromolecule anabolism and active transport are also ATP dependent, as are phosphorylation reactions in intracellular regulatory and signalling pathways [71]. By monitoring and protecting ATP availability, energy systems effectively avoid the cessation of vital cell processes [69]. Even under extreme exercise conditions, the observation that skeletal muscle ATP concentration decreases by only 30% to 40% but is never exhausted [73] bears testament to both the significance of maintaining cell ATP concentration and the exquisite regulation involved [68]. Three distinct yet integrated processes function as energy supply systems in skeletal muscle and, as in most other tissue, provide a regulated and integrated means of regenerating ATP, together responsible for the rate and yield of ATP supply [72]. In response to ATP utilization these intracellular, enzymatically dependent, exergonic biochemical pathways, which differ in substrates, products and processes, are coupled to the regeneration of ATP [74]. Key features of these processes will be reviewed.

2.1.2.2 Phosphocreatine Splitting

Phosphocreatine (PC) is another high-energy phosphagen molecule present in skeletal muscle [22]. Phosphorylation of ADP from PC and H^+ occurs through rapid catalysis by creatine kinase (CK)—a single chemical reaction and most immediate means of regenerating ATP and yielding creatine (Cr) in the process [69]. As a temporal buffer against a decreased ATP concentration when ATPase activity increases, the phosphorylation of ADP by CK is a near equilibrium reaction [70] with the potential to regenerate ATP many times faster than myosin ATPase utilizes it [75]. The ATP yield from PC splitting is therefore largely a function of ATP demand established by muscle contractile activity [76] and the size of the finite muscle PC store [77]. When the rate of ATP utilization exceeds the rate of its regeneration from PC in skeletal muscle, adenylate kinase, or myokinase, has the potential to rapidly catalyse the conversion of ADP to ATP and adenosine monophosphate (AMP) [75]. In skeletal muscle, ADP, AMP and Cr have several possible fates and perform important intracellular metabolic regulatory functions [22]. The cycling of phosphorylation status between Cr and adenine nucleotides in regenerating ATP is often referred to as the ATP-PC or phosphagen energy system [72].

Skeletal muscle PC concentration approximates 60 to 100 $\text{mmol}\cdot\text{kgdm}^{-1}$ [70], sufficient to regenerate ATP during maximal contractile activity for only a brief period of time before PC stores are significantly depleted [78]. Since every 1 mole of PC is capable of regenerating 1 mole of ATP, the potential ATP supply from all intramuscular phosphagen stores approximates 80 to 120 $\text{mmol}\cdot\text{kgdm}^{-1}$ [68]. If this supply were exhausted in isolation, in principle it would be sufficient to support around 5 to 10 s of maximal muscle contractile activity [18]. As the most rapid buffer against ATP depletion but with a finite store, PC splitting is at its highest rate immediately after maximal muscle contractile activity begins and declines within 2 s thereafter [22]. Average rates of ATP regeneration from PC splitting are approximately 3.0 to 6.0 and 1.0 to 2.0 $\text{mmol}\cdot\text{kgdm}^{-1}\cdot\text{s}^{-1}$ during 10 and 30 s of high intensity dynamic exercise, respectively [77], with a peak rate of approximately 9.0 to 10.0 mmol·kgdm^{-1}·s^{-1} occurring within the first 1 to 2 s of maximal contractile activity [70].

2.1.2.3 Glycolysis

Glycolysis refers to the incomplete breakdown of glucose or glucose 1-phosphate to pyruvate or lactate through a dozen enzymatically controlled reactions in the sarcoplasm which comprise the Embden-Meyerhof chemical pathway, or glycolytic energy system [72]. Skeletal muscle obtains glycolytic substrate from two sources: through receptor-mediated active transport of glucose from the extracellular compartment and subsequent phosphorylation by hexokinase (HK); and through glycogenolysis of intracellular glycogen reserves by phosphorylase (PHOS) yielding units of glucose 1-phosphate [22]. Both processes are under intra- and extracellular control with regulatory mechanisms prioritising glycogenolysis when ATP utilization exceeds its regeneration [70]. Depending on the glycolytic substrate source, glycolysis initially involves the use of one (muscle glycogen) or two (blood glucose) ATP molecules per glucose molecule before yielding four ATP molecules during ensuing reactions [68]. Additionally, nicotinamide adenine dinucleotide (NAD^+) is an essential oxidizing cofactor in glycolysis [75], removing hydrogen through glyceraldehyde 3-phosphate dehydrogenase (GAPDH) activity to form NADH [71]. Glycolysis yields pyruvate, and a fluctuating proportion—largely determined by the pyruvate concentration, pH and NADH:NAD ratio—is continually and reversibly reduced to lactate by lactate dehydrogenase (LDH) using NADH [74], effectively recycling the oxidized form of NAD^+ and enabling continued GAPDH activity, and thus glycolysis [71]. Both pyruvate and lactate represent partially degraded intermediates of carbohydrate metabolism with several possible intra- and extracellular fates [74]. Several enzymes in the glycolytic ATP regeneration pathway are regulatory and susceptible to allosteric modulation [71]. While PHOS and phosphofructokinase (PFK) have traditionally been considered rate limiting [70], HK, GAPDH, pyruvate kinase (PK) and LDH also catalyse regulated or committed glycolysis reactions in skeletal muscle [71].

Every 1 mole of muscle glycogen-derived glucose 1-phosphate yields 2 moles of pyruvate, 2 moles of NADH and a net gain of 3 moles of ATP [18]. Skeletal muscle glycogen concentration approximates 300 to 600 mmol·kgdm^{-1} but during voluntary high intensity exercise, glycolysis is restricted to accessing only a portion of this potential source of glycolytic ATP regeneration [22]. Glycolysis slows long before the glycogen store is exhausted, implying that glycolytic ATP regeneration rate and yield is limited during high intensity exercise, even if muscle glycogen concentrations are elevated beforehand [70, 78]. Muscle ATP regeneration through glycolysis reaches a peak rate of approximately 5.0 to 10.0 mmol·kgdm^{-1}·s^{-1} after 5 to 10 s of maximal contractile activity and remains fully stimulated for only several seconds [77]. This may be due to attenuated glycolytic enzyme activation secondary to reduced ATP utilization and/or inhibition of glycolytic enzyme activity [76]. Assuming that around 50 to 100 mmol·kgdm^{-1} of the muscle glycogen store is accessible for glycolysis during high intensity exercise, total glycolytic capacity for ATP regeneration approximates 150 to 300 mmol·kgdm^{-1} [22, 77], roughly 3- to 4-fold that of PC splitting alone [18], and theoretically sufficient ATP to sustain skeletal muscle contractile activity for around 20 to 30 s if used exclusively [20].

2.1.2.4 Oxidative Phosphorylation

The tricarboxylic acid (TCA) cycle is a series of mitochondrial chemical reactions which completely oxidizes two-carbon acetyl group fragments derived from the catabolism of macronutrient molecules [71]. In the case of carbohydrate, the fate of most glycolysis-derived pyruvate in skeletal muscle is translocation to the mitochondrial matrix followed by irreversible oxidative decarboxylation via pyruvate dehydrogenase (PDH), yielding acetyl coenzyme A (acetyl-CoA), NADH and carbon dioxide (CO_2) [74]. For lipid molecules, fatty acids obtained from the extracellular compartment or from intramuscular triglyceride are converted to fatty acyl-CoA and, following mitochondrial translocation, undergo beta-oxidation to yield acetyl-CoA, while extracellular-derived ketones are also a potential substrate [72]. Finally, acetyl-CoA, pyruvate or TCA cycle intermediates are also formed from the deamination or transamination of amino acids following protein catabolism [68]. While skeletal muscle protein turnover is ongoing, amino acids fulfil mainly an integrated function in ATP regeneration through TCA cycle intermediate exchanges [67] and only contribute significantly to total ATP yield during periods of limited carbohydrate availability and/or unusually long duration exercise, when regulatory mechanisms increase their oxidization [69]. The TCA cycle is the common metabolic pathway for acetyl-CoA processing irrespective its macronutrient origin [22], with carbohydrate and fat derivatives the major substrate sources of acetyl-CoA [68].

Nine sequential, enzymatically controlled steps comprise the TCA cycle [71]. Synthesis of citrate from oxaloacetate and acetyl-CoA by citrate synthase (CS) is followed by progressive decarboxylation and oxidation which completely dismembers the acetyl group and reforms oxaloacetate, permitting continued TCA cycle activity [68]. Carbon atoms are removed as CO_2 molecules which diffuse to the extracellular compartment while hydrogen is removed by the oxidizing cofactors NAD^+ and flavin adenine dinucleotide (FAD) in four dehydrogenase reactions [71]. Substrate level nucleotide phosphorylation in the TCA cycle produces an equivalent net gain of one ATP molecule per acetyl group processed [18]. In addition to PDH, CS, isocitrate dehydrogenase (IDH) and alpha-ketoglutarate dehydrogenase (KDH) catalyse key or irreversible reactions in TCA cycle activity and are considered regulatory of the process [71].

The reducing agents NADH and $FADH_2$, formed by GAPDH activity in glycolysis, PDH, and TCA cycle dehydrogenase activity, interact with a series of cytochromes—four metal ion containing protein complexes located on the inner mitochondrial membrane [21]—and are stripped of their acquired protons and associated electrons [67]. The electrons are transferred down an electrochemical gradient along the cytochrome chain to be accepted by oxygen (O_2) [74] which subsequently attracts positively charged protons and is reduced to water (H_2O) through cytochrome oxidase (CO) activity [18]. The oxidized forms of NAD^+ and FAD are thereby recycled, enabling continued TCA cycle dehydrogenase reactions [67]. Commonly referred to as the electron transfer chain (ETC), the cytochrome oxidation pathway serially triggers protons to be actively transported from the matrix to the intermembrane space of the mitochondrion at three complexes in the chain [71]. The resulting electrochemical gradient, or chemiosmotic pressure, established across the inner membrane drives proton diffusion at protein portals on the inner mitochondrial membrane—the ATP synthase complexes [74]. Harnessing the associated proton motive force [22], ATP synthase combines protons with P_i to drive the phosphorylation of ADP to ATP and H_2O [71]. The process is appropriately known as electron transport-mediated oxidative phosphorylation [22].

The rate of ATP regeneration via oxidative phosphorylation in skeletal muscle is a complex result of allosteric modulation of mitochondrial enzyme activity and changing concentrations of substrates, coenzymes and O_2 [67]. Estimations place the maximum rate of mitochondrial ATP regeneration at approximately 2.8 and 1.0 $mmol \cdot kgdm^{-1} \cdot s^{-1}$ from exclusive carbohydrate or fat oxidation respectively [22], the lowest rate of ATP regeneration among the energy systems in skeletal muscle [18]. Nonetheless, the capacity for ATP regeneration through oxidative phosphorylation is large, owing to the quantity and diversity of macronutrient molecules available to obtain precursor acetyl groups and the high ATP yield from complete oxidation of each substrate molecule [67]. These same factors make total potential ATP yield from this energy system difficult to estimate [79]. Complete mitochondrial oxidation of 1 mole of pyruvate and the NADH initially produced with it in glycolysis yields 15 to 18 moles of ATP [68] while 1 mole of the typical saturated fatty acid palmitate, yields 129 to 131 moles of ATP [67]. The inexact net ATP yields reported in the literature are due to different ATP costs associated with initial substrate processing and/or mitochondrial membrane transport mechanisms [75]. The ATP regeneration capacity from full oxidative phosphorylation of muscle glycogen stores alone represents in excess of 100-fold that of the ATP-PC and glycolytic systems combined [16] or enough ATP to support contractile activity for approximately 60.0 min [68], while the potential ATP yield from fat stores is theoretically capable of supporting many thousands of minutes of muscle force production [22]. Clearly, of the ATP regeneration systems, only oxidative phosphorylation has the capacity to meet the energetic demands of prolonged skeletal muscle contractile activity [72].

2.1.2.5 Aerobic and Anaerobic Energy Supply

As the final electron acceptor in the ETC, mitochondrial O_2 is essential for recycling the limited quantity of oxidizing cofactors NAD^+ and FAD which permits continued TCA cycle activity [67]. Since O_2 is a necessary reactant in oxidative phosphorylation, this energy system is also known as oxidative metabolism, mitochondrial respiration, or the aerobic energy system [72]. For the purposes of this study, aerobic energy supply is considered the metabolic process delivering ATP for biological work, including skeletal muscle contractile activity, through reliance on O_2 utilization in oxidative phosphorylation [71]. By contrast, the first two energy supply processes discussed above are not reliant on O_2 as a reactant, and so its presence or absence is inconsequential to their regeneration of ATP, at least when considered in isolation [80]. Glycolysis and PC splitting are frequently referred to as non-oxidative, O_2-independent, or anaerobic energy systems [18]. In this study, anaerobic energy supply will refer to metabolic processes providing ATP through PC splitting and glycolysis [74]. While anaerobic ATP regeneration is frequently explained on the basis of insufficient O_2 for oxidative phosphorylation, this is considered an outdated, invalid and oversimplified assumption that should be avoided [79]. The rate and yield of anaerobic ATP supply in skeletal muscle during exercise is influenced by many signals other than inadequate O_2 [81]—largely intracellular responses to ATP, PC and glycogen utilization [76] but potentially also extracellular acid-base status [82].

In skeletal muscle, O_2 for ETC activity is derived from the temporary, limited store bound to myoglobin [83]. Peripherally available O_2 also includes that which is dissolved in the extracellular fluid and bound to haemoglobin in red blood cells [24]. In mitochondrial respiration, ADP phosphorylation is driven by oxidation [18] such that aerobic ATP regeneration is coupled to O_2 utilization [71]. All the O_2 utilized for aerobic ATP regeneration is ultimately obtained and delivered from the atmosphere through the combined actions of pulmonary respiration and cardiovascular circulation [60]. Pulmonary O_2 uptake (VO_2) is therefore commonly used to indicate whole-body aerobic ATP supply [81]. Since whole-body O_2 utilization is dependent on both mitochondrial O_2 use and arterial O_2 supply, the rate and magnitude of changes in VO_2 reflect an adjustment in both peripheral O_2 metabolism and systemic O_2 transport [74]. Together with the type of substrate oxidized, these factors determine the rate of oxidative phosphorylation [83]. Assuming, hypothetically, the exclusive oxidation of either carbohydrate or fat, every 1 mole of ATP regenerated aerobically is associated with the utilization of around 3.5 or 4.0 L of O_2 respectively [84]. Expressed differently, for every 1.0 L of O_2 utilized, 19.6 to 21.1 kJ of energy in the form of ATP is supplied aerobically based on the exclusive use of fat or carbohydrate substrate, respectively [74].

Activities of daily living, exercise and sport events differ dramatically in the nature, magnitude and duration of skeletal muscle contractile activity involved, imposing varying demands on ATP regeneration mechanisms [67]. The reported rate and yield of ATP regeneration through PC splitting, glycolysis or oxidative phosphorylation represent estimations based on exclusive and exhaustive use of each energy system—a representation which obscures the integration of energy supply processes [72]. Many studies elucidating the rates and capacities of ATP regeneration mechanisms in skeletal muscle have relied on methods such as isolated muscle fibre preparations, artificially stimulated contractile activity, or chemical blockade of alternative energy systems [21], methods long acknowledged as potentially not reflective of *in vivo* conditions [85]. Further, human movement is more complex than muscle contractile activity, involving the coordinated, non-uniform involvement of skeletal muscle and profound systemic responses [81]. It is reasonable to suggest that aerobic and anaerobic energy system rate and yield varies between muscle sites depending on contractile demand, fibre type and substrate availability, among other things [65]. As Gollnick & Hermansen [85] suggested over forty years ago, metabolic changes occurring in muscle should be seen as the sum or mean of changes occurring in many different motor unit pools at the same time rather than as a single, uniform process.

2.1.2.6 Energy System Regulation

An exhaustive appraisal of energy system regulation is beyond the scope of this research problem and several detailed reviews of the theme are available [20-22, 66-68]. However, subsequent sections describing aerobic and anaerobic energy supply during maximum effort exercise require appreciation of the biological mechanisms by which the rate and yield of ATP regeneration processes change during acute exercise.

The intracellular ratio between the concentrations of high-energy phosphagen molecules (ATP, ADP and AMP) describes the energy state, adenylate charge or phosphorylation potential of a muscle fibre [71]. Altered phosphagen molecule ratios modulate the activity of enzymes in each of the ATP regeneration processes, including CK (PC splitting), PHOS (glycogenolysis), PFK, PK and LDH (glycolysis), PDH, CS and IDH (TCA cycle), and CO (ETC) [66, 68-71]. Mitochondrial enzyme activity is particularly sensitive to a reduced ATP:ADP ratio, while a reduced ATP:AMP ratio, characteristic of a very low energy state, stimulates PHOS and PFK, accelerating glycogenolysis and glycolysis respectively, and preferentially increasing carbohydrate utilization [75]. In this way, stimulation of both sarcoplasmic substrate phosphorylation and mitochondrial oxidative phosphorylation are inversely proportional to cell energy state [68].

Reversible binding of allosteric effectors in response to altered contractile activity and/or cell energy state in skeletal muscle may stimulate or inhibit enzyme activity, directly by coenzymes or cofactors, or indirectly through protein kinases or phosphatases [21]. Allosteric stimulation by inosine monophosphate (IMP; PHOS), P_i (HK, PHOS and CO), ammonium ion (NH_4^+; PHOS and PFK), H^+ (LDH and PDH), and Ca^{2+} (PHOS, PDH, IDH and KDH) accelerates the activity of enzymes involved in aerobic and anaerobic ATP regeneration [66, 68-71]. Conversely, glucose 6-phosphate (HK and PHOS), H^+ (PHOS and PFK), citrate (PFK, PDH and CS), and PC (PFK and PK) inhibit key energy system enzymes and moderate ATP regeneration processes [66, 68-71]. The stimulation of glycogenolysis and mitochondrial oxidation by Ca^{2+} is particularly elegant since it implies that Ca^{2+} is effectively involved in both initiating muscle contractile activity and stimulating aerobic and anaerobic ATP regeneration [71].

Mitochondrial reduction-oxidation (redox) state is reflected by the $NADH:NAD^+$ concentration ratio and in skeletal muscle it varies in parallel with contractile activity since increased glycolytic and TCA cycle flux raise the $NADH:NAD^+$ ratio [75]. An increased redox state stimulates sarcoplasmic LDH activity but inhibits mitochondrial TCA cycle dehydrogenase enzyme activity, effectively prioritising glycolysis and lactate formation over oxidative phosphorylation [71]. In mitochondrial respiration, disinhibition of TCA cycle dehydrogenase enzymes is O_2 dependent—

an increased intracellular O_2 concentration stimulates CO, accelerating ETC activity and oxidation of NADH, disinhibiting TCA cycle activity and aerobic ATP regeneration [20]. Regulation of skeletal muscle redox state and oxidative phosphorylation has been the source of much debate and theoretically depends on: 1. mitochondrial enzyme activity and TCA cycle substrate availability, largely dictated by cell energy state and associated metabolic responses; and 2. O_2 availability and influence on ETC activity, largely dictated by respiratory acquisition and cardiovascular delivery of O_2 to active muscle [68, 83, 86].

During exercise, changes in neurotransmitter and hormonal concentrations act directly or indirectly to increase macronutrient catabolism and support increased ATP regeneration processes in skeletal muscle [68]. For example: epinephrine and glucagon activate hormone-sensitive lipase (HSL) and lipoprotein lipase (LPL), thereby increasing fatty acid availability for mitochondrial oxidation and aerobic ATP regeneration [72]; epinephrine and norepinephrine augment glucagon and suppress insulin secretion at the pancreas and thereby indirectly promote substrate mobilization rather than storage [69]; and elevated catecholamine concentrations augment the activation of PHOS and consequently glycogenolysis [67]. In this way, neuroendocrine responses mediate changes in aerobic and anaerobic energy system flux and substrate use at different sites (skeletal muscle, liver, adipose tissue) that promote enhanced skeletal muscle ATP regeneration [69]. Additionally, muscle cytokines (e.g. interleukin 6; IL-6), in response to low cell energy state and/or low substrate availability act peripherally to accelerate carbohydrate and fat catabolism and centrally as key intermediaries between muscle contractile activity and associated neuroendocrine responses [67].

Since aerobic and anaerobic ATP regeneration mechanisms are substrate dependent, the concentrations of macronutrient or metabolic intermediate molecules in skeletal muscle influences energy system rate and yield [26]. For example, a glycogen concentration below 100 $\text{mmol}\cdot\text{kgdm}^{-1}$ impairs glycolysis and consequently pyruvate formation, slowing both glycolytic and mitochondrial ATP supply [78]. Conversely, during periods of extensive glycolytic activity, feedforward stimulation of PDH by a rising pyruvate concentration accelerates acetyl-CoA formation and aerobic ATP regeneration [81]. Likewise, since ATP and PC concentrations in skeletal muscle are limited it is plausible that availability of these substrates for ATPase and CK respectively influences anaerobic energy supply during contractile activity [26]. Beyond intracellular regulation of ATP regeneration, energy system metabolites and substrates interact systemically also [80]. For example, H^+ and lactate released from skeletal muscle suppress lipolysis at adipose tissue, thereby limiting extracellular fatty acid availability for muscle aerobic ATP regeneration during high intensity exercise [68].

Finally, different skeletal muscle fibre types mean that mechanisms regulating the rate and extent of aerobic and anaerobic ATP regeneration are not uniform throughout active muscle [65]. Similar fibre types in a skeletal muscle are grouped in motor units innervated by smaller, lower threshold (type I fibres) or larger, higher threshold (type II fibres) motor neurons such that progressively greater neural stimulation cumulatively adds larger motor units to the recruited fibre pool [87]. Differences in contractile (e.g. myofibril content and specific tension) and metabolic (e.g. enzyme concentration, isoform and activity) properties of fibre types implies that neuromuscular recruitment concurrently influences both absolute intensity and duration of skeletal muscle force production, ATP utilization, and ATP regeneration through energy system responses and substrate utilization [68]. For example, type II fibres typically display higher myosin ATPase, CK and PHOS activity and higher PC and glycogen concentration, preferentially suited to ATP regeneration through anaerobic mechanisms, while type I fibres are typically predisposed to aerobic ATP regeneration owing to higher mitochondrial and myoglobin content, CS and IDH activity, triglyceride concentration and capillary density [24, 68, 87].

The simultaneous influence of these energy system regulatory mechanisms confers an overlapping, interrelated and dynamic nature to aerobic and anaerobic ATP supply in skeletal muscle [77]. Activity of all ATP regeneration mechanisms is dependent on a change in ATP utilization largely dictated in skeletal muscle by the nature of contractile activity [67]. In general, chemical feedforward and feedback signals to changes in ATP utilization alter energy system activity, or flux, altering the rate of ADP phosphorylation [69]. The aerobic and anaerobic supply of ATP during rest or exercise represents the net effect of these simultaneously operational intra- and extracellular regulatory mechanisms [74].The same stimuli for muscle contractile activity—Ca^{2+} release from SR and ATP hydrolysis by ATPase—establish muscle ATP utilization and initiate the change in serial and shared metabolic mediators of the aerobic and anaerobic energy systems [67, 75]. In this way, an ATP demand is coupled to a response in the rate and yield of ATP regeneration [80].

2.1.2.7 Summary

Energy systems refer to intracellular chemical processes that monitor and protect ATP availability, coupling ATP utilization to ATP regeneration to maintain the potential energy for biological work [69]. Anaerobic energy systems do not require O_2 as a reactant and are able to regenerate large amounts of ATP per unit time from sarcoplasmic PC splitting and glycolysis but are limited in rate and yield during a single bout of exercise [26]. Aerobic ATP regeneration relies on O_2 as a reactant and uses carbohydrate, lipid and protein derivatives as substrates for a hypothetically unlimited yield of ATP via mitochondrial oxidative phosphorylation, but at a limited rate [72]. In skeletal muscle, rapid and substantial fluctuations in ATP demand, the simultaneous interdependent influences on ATP supply, and the different contractile and metabolic properties of fibre types make energy system regulation complex [81]. Driven by ATP utilization which is largely determined by contractile activity, feedforward and feedback regulation of aerobic and anaerobic energy systems by intra- and extracellular mechanisms adjust ATP supply in response to muscle energetic demands [87].

2.1.3 Aerobic and Anaerobic Energy System Responses during Exercise

2.1.3.1 Background

Attempts at classifying exercise based on the primary source of ATP supporting muscle contractile activity appear to have started when Fox *et al*. [40] proposed the allocation of maximum effort exercise tasks into one of four domains based on completion time. Models describing the relative involvement of aerobic and anaerobic energy supply across a range of exercise performance durations were introduced by Åstrand & Rodahl [88] and Mathews & Fox [89]. According to Gastin [9], reproduction of these initial interpretations over subsequent decades may have contributed to common misconceptions regarding the responses of ATP regeneration mechanisms during exercise. These include: 1. that energy supply mechanisms respond to muscle ATP demand sequentially in distinct time periods based on exercise duration and/or serial exhaustion of ATP regenerating capacity by each system; and 2. that aerobic energy supply responds slowly to an increased muscle ATP demand and contributes insignificantly to ATP supply during short duration high intensity exercise [9]. These misconceptions will be addressed within a review of current information on the responses of aerobic and anaerobic ATP regeneration during dynamic, whole-body exercise.

2.1.3.2 Energy System Interaction

Evidence that no single energy system is used exclusively during exercise is provided by several observations. Firstly, biopsy studies have revealed that muscle lactate production and by implication glycolytic ATP regeneration, accelerates from the onset of high intensity exercise and not only once PC stores are depleted [78, 90]. Secondly, the compensatory nature of energy systems as ATP buffer mechanisms is clear from the significant enhancement in VO_2 at the start of an exercise bout when preceded by warm-up exercise or blood flow occlusion, conditions which reduce muscle PC concentration and/or peripheral O_2 stores [91]. Thirdly, it has been demonstrated that muscle contraction with blood flow occlusion sufficient to restrict O_2 supply and oxidative phosphorylation limits glycolytic ATP regeneration capacity by around 33% [70], supporting the contention that full utilization of the capacity for anaerobic ATP supply is at least partially dependent on aerobic energy system activity [81]. While aerobic and anaerobic ATP supply mechanisms are considered distinct based on chemical reactions, relative contributions during different types of exercise and sensitivity to specific exercise training [72], ignoring the functional interdependence between the energy system responses during exercise constitutes an oversimplification [9].

2.1.3.3 Aerobic Energy Supply Responses

Oxidative phosphorylation is stimulated at the onset of muscle contractile activity [67]. While providing an immediate source of O_2 for skeletal muscle aerobic ATP regeneration [92], peripherally available O_2 in physical solution or bound to haemoglobin and myoglobin is inadequate to meet muscle ATP demand [24]. However, utilization of these temporary stores when skeletal muscle ATP demand increases does lower the O_2 tension in blood [92], thereby establishing a larger O_2 partial pressure gradient between alveolar and pulmonary capillary blood [60]. At the start of high intensity exercise it may take approximately 10 s for venous blood to reach the pulmonary circulation, briefly delaying the acceleration in VO_2 following the onset of increased muscle O_2 utilization [83]. Ultimately, VO_2 largely reflects the rate of O_2 transfer from environment to blood secondary to O_2 utilization [79] because the transfer is somewhat dependent on the magnitude of the O_2 partial pressure gradient established by muscle O_2 utilization [92]. While the exact relationship between muscle O_2 utilization and VO_2 has been debated for almost a century [93, 94], during the transition from a lower to a higher muscle power output, VO_2 underestimates O_2 utilization by working muscle for a period of time [92].

Modern measurement systems permitting breath-by-breath monitoring of pulmonary respiration have allowed closer scrutiny of VO_2 kinetics—the time course of VO_2 responses [9]. At the start of dynamic exercise VO_2 shows an exponential increase with a half-time, task dependent, of around 20 s [83]. This acceleration in VO_2 implies that contrary to popular belief, aerobic ATP regeneration increases rapidly following the onset of muscle contractile activity [81]. After approximately 20 to 30 s of all-out effort exercise, the rapidly rising rate of oxidative phosphorylation renders aerobic energy supply the dominant ATP regeneration method during continued contractile activity [63]. The magnitude and duration of the exponential rise in VO_2 at the onset of exercise is a function of exercise intensity [94] such that VO_2 may reach around 90% of maximum during high intensity exercise lasting only 30 to 60 s [95]. Short duration high intensity exercise has been shown to elicit maximum VO_2 (VO_{2max}) after only 60 s [96, 97]. The traditional views of aerobic ATP supply as slow to respond and insignificant during high intensity exercise should thus be reconsidered [9].

2.1.3.4 Oxygen Deficit

Despite the exponential rise in VO_2 at the onset of exercise, O_2 utilization and oxidative phosphorylation do not instantaneously attain rates that can meet skeletal muscle ATP demand [81]. The physiological inertia of systemic responses which increase O_2 supply and/or the metabolic inertia of peripheral stimulation of mitochondrial O_2 utilization have been offered as explanations for this [83, 86]. As respective examples, elevated O_2 supply is dependent on profound cardiovascular and respiratory adjustments under complex feedforward and feedback neural and humoral control [83], while elevated O_2 utilization is dependent on increased availability of acetyl groups from accelerated carbohydrate and lipid catabolism [86]. Regardless of the degree to which it is determined by O_2 supply and/or O_2 utilization [94] the acceleration in aerobic ATP regeneration is delayed in comparison to the immediate, exercise-induced change in muscle ATP utilization [81]. Wherever ATP demand exceeds momentary aerobic ATP supply, the energy demand of biological work is met by a combination of aerobic and anaerobic ATP regeneration [27]. In VO_2 kinetics this phenomenon is termed the O_2 deficit—the difference between measured VO_2 and the VO_2 demand for a given intensity of exercise [98]. The O_2 deficit occurs transiently during the initial period of submaximal intensity exercise but persists during higher intensity exercise [27]. It implies that anaerobic energy supply is accounting for the difference between ATP demand and O_2-dependent aerobic ATP supply [98].

2.1.3.5 Steady-State Oxygen Uptake

During most forms of submaximal intensity exercise VO_2 generally shows no further increase after its initial exponential rise levels off [99], attaining a relative plateau within 3.0 to 5.0 min [100]. A steady rate of VO_2 may be maintained for prolonged periods of exercise at intensities below ventilatory threshold under cool, dry environmental conditions [99], and this is frequently referred to as steady-state exercise, or aerobic exercise [60]. Steady-state is considered a condition in which parameters reflective of whole-body aerobic ATP regeneration, such as heart rate (HR), ventilation and VO_2 do not change appreciably over a period of time [18], implying that VO_2 reflects whole-body O_2 utilization [67]. For a given submaximal intensity of exercise, once a steady-state has been achieved, O_2 deficit is suspended and the ATP demand of continued exercise is supplied aerobically through oxidative phosphorylation [83]. Consequently, provided a steady-state is attained, aerobic energy supply as indicated by VO_2 above resting requirements represents the total energy expenditure of exercise for a given submaximal intensity [79]. It has been suggested that following the attainment of steady-state, PC breakdown and regeneration is balanced and a relative steady-state exists as far as muscle phosphagen molecule concentrations are concerned, with levels maintained until a different ATP demand is imposed [75]. As di Prampero [65] pointed out though, such a condition does not imply that a true steady-state is present in all active skeletal muscle, since intramuscular fuel stores and consequently the peripheral respiratory quotient—the ratio between CO_2 production and O_2 utilization—change as exercise proceeds, and likely differ between regions of the same active muscle. Over a range of submaximal exercise intensities the steady-state VO_2 obtained after 3.0 to 5.0 min is a linear function of exercise intensity [65].

2.1.3.6 Slow Component of Oxygen Uptake

In some instances, during continued exercise a constant submaximal intensity, VO_2 continues to increase above the plateau attained in the initial 3.0 to 5.0 min period [101], with this upward drift being referred to as the slow component of VO_2 [67]. The slow component is generally considered to begin approximately 90 to 150 s after the onset of moderate to high intensity exercise [101]. The size of the slow component is proportional to relative exercise intensity—typically larger during exercise at intensities above ventilatory threshold [102]. Likely causes of this rising ATP demand in the face of constant external power output include: altered substrate utilization; increased thermogenic effect of rising core temperature and catecholamine concentrations; increased ion and metabolite transport and metabolism; increased cardiac and respiratory muscle contractile activity; recruitment of less efficient motor units; and progressive involvement of auxiliary musculature [101]. Exercise involving a considerable slow component complicates the use of VO_2 for the interpretation of energy expenditure [103].

2.1.3.7 Maximum Oxygen Uptake

During exercise of increasing intensity VO_2 rises concomitantly to a measurable maximum, representing the highest rate of whole-body O_2 utilization for aerobically regenerating ATP in a given exercise modality [79]. The associated intensity of exercise is termed maximum aerobic power [104]. The interpretation of VO_{2max} has been a major theme of debate in the scientific literature, with the factors limiting the highest attainable VO_2 during exercise being central to the argument [8, 105, 106]. It is still unclear to what degree and under what circumstances VO_{2max} is limited by altered neuromuscular recruitment dictating skeletal muscle contractile activity, ATP utilization and thus mitochondrial O_2 demand, and/or approaching limits to the systemic and local capacity for O_2 supply [83, 86]. What is clear is that within a given modality and format of voluntary exercise, a measurable maximum rate of aerobic ATP regeneration, as reflected by VO_{2max}, is attained [107].

2.1.3.8 Anaerobic Energy Supply Responses

During high intensity exercise a steady-state VO_2 is not attained since power output exceeds that which can be supported by aerobic ATP supply alone [100]. Rather, VO_2 continues to increase until the termination of exercise or a significant reduction in skeletal muscle ATP demand [101]. While aerobic energy system activity increases rapidly in response to high intensity exercise [94] the maximum rate of aerobic ATP regeneration during voluntary exercise, as reflected by VO_{2max}, remains inadequate to meet total energy demand [84]. The additional energy requirement is met by anaerobic energy supply [80]. In other words, beyond simply supplying ATP rapidly during the initial period of an exercise bout, anaerobic energy systems continue to contribute to the large ATP demand during exercise involving high muscle power output [70]. Consequently, during high intensity exercise the O_2 deficit continues to increase until task completion, exhaustion, or a decrease in power output, depending on the format of exercise [27, 108-110].

Anaerobic energy supply mechanisms regenerate ATP at a higher rate than aerobic mechanisms [70]. The ratio of maximum anaerobic ATP supply rate to maximum aerobic ATP supply rate during exercise is in the range of 2.0 to 2.6 based on mathematical modelling of running performance [25], while others have suggested a ratio between 2.0 and 4.0 based on muscle metabolic measurements [77]. While the maximum rate of anaerobic ATP supply in muscle is no longer considered the limiting factor in very brief (< 5-10 s) maximal intensity exercise activities like sprinting, throwing, jumping and weightlifting [76], anaerobic energy systems do supply the majority of ATP regenerated during these types of activities [9]. Maximum intensity weightlifting and short duration sprint exercise are examples of activities involving power outputs which are estimated to be 10- to 20-fold and 3- to 5-fold that of maximum aerobic power, respectively [111].

2.1.3.9 Anaerobic Capacity

The muscle power output characterizing short duration high intensity exercise is not matched during longer duration bouts [77]. For a given exercise modality, maximum effort exercise bouts with performance durations from 1 or 2 s up to approximately 300 s routinely display the steepest drop in average power output, with steeper declines nearer shorter exercise durations on the performance time continuum [76]. Additionally, the final power output sustainable near the end of all-out effort exercise lasting 90 s or more appears similar to that capable of being supported by aerobic energy supply alone [112]. These phenomena support the idea that while anaerobic energy supply is essential for regenerating ATP at a high rate in skeletal muscle, there exists a finite accessible capacity for anaerobic energy supply during a given bout and modality of exercise [9, 76]. While early theories suggested an inhibition of anaerobic ATP supply during high intensity exercise [113], contemporary information suggests that anaerobic energy yield during short duration high intensity exercise is limited by muscle ATP demand [76]. More specifically, reductions in motor unit recruitment, cross-bridge force generation and/or SR Ca^{2+} cycling during high intensity exercise may slow muscle ATP utilization and consequently the formation of allosteric stimulators of anaerobic ATP supply [114].

Whether restricted by attenuated ATP demand or by inhibition of continued ATP supply, the lack of a universal definition for the available or realized anaerobic yield during exercise has long been bemoaned [115]. For the purposes of this study, anaerobic capacity will refer to the maximum amount of ATP resynthesized by the sum total of whole-body anaerobic energy supply mechanisms during a specific maximum effort exercise task [82]. Since the rate and yield of anaerobic energy supply in skeletal muscle is likely limited, anaerobic capacity denotes a measureable quantity, expressed in energy (kJ) or energy equivalent (e.g. O_2 equivalent; L O_2 eq) terms [98]. Anaerobic capacity should not be confused with anaerobic work capacity—the external power output (W) maintained or the mechanical work (kJ) completed during a specific high intensity exercise task attributable to anaerobic energy supply [23]. Anaerobic attributable energy supply is another distinct construct, representing the energy yield during exercise provided by anaerobic ATP regeneration mechanisms [82], expressed in energy (kJ) or energy equivalent (L O_2 eq) terms, or frequently as the proportional (%) contribution to total energy demand [98]. Factors determining anaerobic capacity, anaerobic work capacity and anaerobic attributable energy supply, as well as appropriate methods for measuring these constructs, remain debated in the scientific literature [23, 27, 76].

2.1.3.10 Summary

Skeletal muscle aerobic ATP supply increases exponentially at the onset of exercise, initially making use of peripherally available O_2 while systemic cardiorespiratory mechanisms adjust rapidly, increasing O_2 supply [92]. High intensity exercise stimulates anaerobic energy supply in skeletal muscle which despite a high maximum rate of ATP regeneration, is limited in capacity [72]. During exercise at a submaximal intensity, the rate of aerobic ATP regeneration is a determinant of the skeletal muscle power output and associated ATP utilization that can be maintained for prolonged periods [76]. When a steady-state VO_2 does not occur during exercise, skeletal muscle anaerobic ATP supply contributes to total energy demand, and an O_2 deficit is observed in VO_2 kinetics [110]. The different rates and capacities of ATP regeneration mechanisms in skeletal muscle do not imply exclusivity in response to the energetic demand of most exercise tasks [9]. Rather, significant overlap and interdependence exists between aerobic and anaerobic energy supply [81].

2.1.4 Factors Influencing Energy System Involvement during Exercise

2.1.4.1 Theoretical Framework

Since absolute expressions of muscle power output display large variations between individuals and exercise modalities, exercise intensity is best described using indicators relative to the exercise capacity of an individual [79]. For example, submaximal and supramaximal intensity exercise describes power output below and above maximum aerobic power respectively, specific to a given individual [111]. These descriptors of exercise intensity should not be confused with the definition of maximum effort exercise provided at the beginning of this chapter. Additionally, two methods of describing energy system involvement and relative contribution during exercise can be distinguished. The proportional contribution made by aerobic and anaerobic energy supply to the total energy demand during an exercise task is most commonly reported, typically for an entire distinct bout of maximum effort exercise [16, 19, 24, 60, 68, 85]. For example, aerobic and anaerobic ATP supply during a specific exercise task lasting 50 s may be reported as representing approximately 40% and 60% of total energy demand respectively [9]. **Figure 2.1** provides a model illustrating such a representation. Importantly, since ATP supply from each energy system is not constant throughout an exercise bout, these models do not reflect the time course or magnitude of change in aerobic and anaerobic ATP supply during an exercise bout [9]. Characterizing the kinetics of absolute or relative aerobic and anaerobic energy supply during the course of an exercise task requires that energy system contributions be measured and expressed over sequential phases within the duration of the task [63, 73, 110].

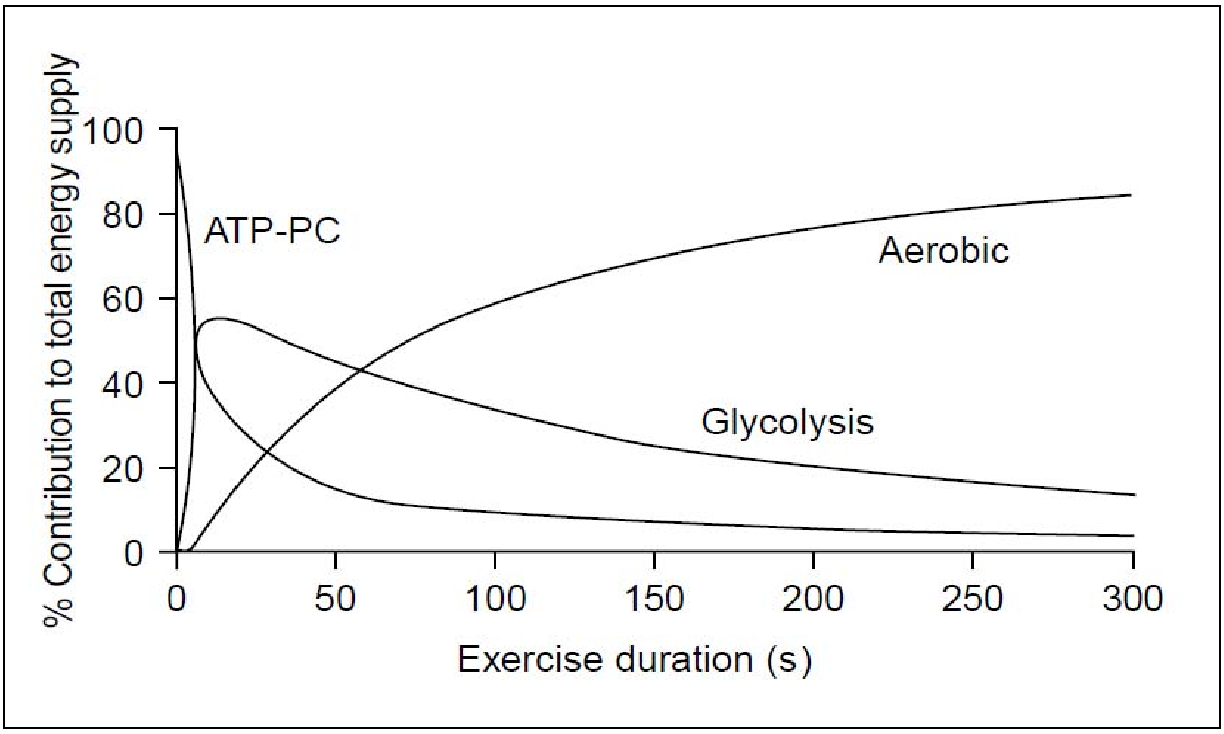

Figure 2.1: Relative aerobic and anaerobic energy system contribution to total energy supply during distinct, maximum effort exercise bouts of various durations. Anaerobic energy supply has been separated into phosphagenic and glycolytic contributions.

Abbreviations: **ATP-PC** phosphagen splitting component of anaerobic energy supply.

Note: Figure from Gastin [9].

2.1.4.2 Short Duration Exercise

Short duration maximum effort exercise bouts are performed at supramaximal intensity, characterized by high muscle power output from considerable high-threshold motor unit recruitment and extensive skeletal muscle involvement [76]. Unsurprisingly, muscle anaerobic energy supply mechanisms are powerfully stimulated with PC splitting and glycolysis regenerating ATP rapidly during this type of exercise [9]. Each contributes close to 50% of total energy supply during a 5 s all-out effort exercise task, while the relative energy contribution from phosphagen sources is even greater in exercise tasks of shorter duration [77]. Glycolysis is most powerfully stimulated in all-out effort exercise tasks lasting 5 to 30 s and contributes the largest single proportion (40-60%) to total energy demand in exercise bouts with performance durations of between approximately 5 and 60 s [72]. Intramuscular glycogen stores are the predominant source of glycolytic substrate during this type of exercise [70]. Maximum effort exercise bouts lasting 10 s are supported by relative anaerobic energy contributions of approximately 95% [97, 116], while the corresponding value for exercise performances lasting 30 s is approximately 70% to 75% [84, 97, 117-119]. Clearly, short duration maximum effort exercise tasks are proportionally dominated by anaerobic energy supply mechanisms [25].

2.1.4.3 Long Duration Exercise

Long duration maximum effort exercise tasks are performed at submaximal intensity such that muscle contractile energy demand is largely sustainable by the rate of, and capacity for, skeletal muscle aerobic ATP supply [76]. In comparison to short duration exercise, less extensive skeletal muscle recruitment of predominantly low-threshold motor units restricts both muscle ATP utilization and the stimulation of anaerobic energy systems during submaximal intensity exercise [68]. The duration and relative intensity of this type of exercise dictates the utilization of carbohydrate and lipid molecules as substrates for substantial acetyl-CoA oxidization and a large aerobic ATP yield [72]. Oxidative phosphorylation can sustain the demand for skeletal muscle ATP regeneration for considerable periods of time during submaximal intensity exercise [9]. However, few empirical measures of relative energy system contributions during exercise performances lasting 10.0 min or longer have been made. Duffield *et al*. [120] reported relative aerobic energy system contributions during 3000 m running of 86% to 93% for males (mean performance time ≈ 9.5 min) and 92% to 94% for females (mean performance time ≈ 11.5 min). Weyand *et al*. [121] reported that aerobic energy supply accounted for 96% and 97% to the total energy demand during a 5000 m run in men (mean performance time ≈ 15.5 min) and women (mean performance time ≈ 19.0 min) respectively. Mathematical models of the energetics of world record running performances support these measures, with estimated aerobic contributions of 92% to 93% for exercise performance durations of approximately 13.0 min and higher proportional aerobic contributions in events with longer performance durations [122].

2.1.4.4 Intermediate Duration Exercise

Empirical evidence [63, 110, 119, 123-126] and mathematical modelling [122, 127] has shown that distinct exercise bouts lasting longer than approximately 90 to 100 s are proportionally dominated by aerobic ATP regeneration and that relative aerobic energy supply contribution during the bout increases over time. Maximum effort exercise lasting several minutes has consistently been shown to induce VO_2 values that reach and remain at or near VO_{2max} within 60 to 90 s [36, 39, 85, 96, 97, 118, 128], reflecting a high rate of ATP regeneration from the aerobic energy system. Indeed exercise tasks with performance durations of approximately 5.0 min elicit aerobic contributions of around 85% of total energy supply based on measurements made during cycling [129], kayaking and swimming [114], results supported by mathematical modelling [127].

While intermediate duration maximum effort exercise tasks last for several minutes, mean power output frequently matches or exceeds maximum aerobic power owing to considerable low- and high-threshold motor unit involvement [63]. Sport events in this category are characterized by fast starts, breakaway efforts and end spurts which elicit significant skeletal muscle anaerobic ATP regeneration [23, 125, 130]. Gollnick & Hermansen [85] were among the first to recognize that despite powerful stimulation of anaerobic ATP supply, short duration (< 60-90 s) high intensity exercise is too brief to fully exhaust anaerobic capacity, results corroborated in several studies [97, 119, 131-133]. By contrast, maximum effort exercise performances lasting 2.0 to 10.0 min have been shown to elicit maximum anaerobic energy yield [36, 98, 109, 129, 132, 134]. Further, results of a mathematical analysis of running performances over distances from 1500 to 10000 m by Ward-Smith [122] suggest that the absolute anaerobic attributable energy yield is constant and independent of running distance, at least within the range of distances studied. Empirical data supports this contention. Craig *et al*. [129] found no significant difference in anaerobic energy yield between ergometer cycling bouts conducted over 2.0 or 5.0 min despite differences in average power output. Foster *et al*. [109] corroborated these results in cycling time trials over 500, 1000, 1500 and 3000 m. In all but the shortest exercise bout, the absolute anaerobic attributable energy yield did not vary with distance. Spencer & Gastin [63] obtained similar results for running exercise bouts of 400 to 1500 m. While the proportional contribution of anaerobic ATP supply to total energy demand in maximum effort exercise is lower in performances with longer durations, the same total capacity for anaerobic energy supply appears to be accessible, at least in athletes performing intermediate duration exercise events [135]. These results are consistent with: 1. the existence of an individual maximum for anaerobic energy supply within a given exercise modality; and 2. a large energy yield from anaerobic ATP regeneration during maximum effort exercise bouts with performance durations between approximately 2.0 and 10.0 min [23, 63]. Foster *et al*. [135] and Losnegard *et al*. [136] have suggested that in events with performance durations within this range, the capacity for anaerobic energy supply and its distribution during events rather than VO_2 may be the discriminating factor between highly trained athletes.

Evidence suggests that maximum effort exercise bouts lasting around 60 to 75 s likely produce aerobic and anaerobic energy supply contributions of roughly equal magnitude [63, 119, 123-127, 133], a shorter duration than traditionally purported. For example, a popular exercise physiology text has suggested aerobic and anaerobic contributions during performances lasting 2.0 min to be 40% and 60% respectively [19], while another purports equal proportions of aerobic and anaerobic energy contributions in exercise bouts lasting approximately 3.5 min [16]. Anaerobic energy yield during intermediate duration maximum effort exercise appears to be overestimated in these models. These texts may have perpetuated information based on early investigations [38-40] or models [88, 89] of the theme. Most early investigations used techniques for assessing anaerobic energy supply that are now considered of questionable validity [26], while some early models used assumed rather than measured values for aerobic (e.g. 5.0 $L \cdot min^{-1}$) and anaerobic (e.g. 125 to 200 kJ) energy supply capacity to estimate relative energy system contributions [24, 85]. According to Ward-Smith [25], some traditional models of energy system contribution during exercise overestimate aerobic contribution for very short duration (< 10 s) tasks and overestimate anaerobic contribution for tasks lasting longer than 100 s. The implication is that aerobic energy supply may play a proportionally larger role during intermediate duration sport events than has been widely acknowledged [9, 63, 137].

2.1.4.5 Exercise Modality

Different modalities of exercise involve distinct muscle utilization patterns [25]. The biomechanical demands of an exercise task therefore influence the nature of skeletal muscle energy system stimulation [115]. Submaximal and maximum responses in VO_2, indicative of changes in aerobic energy supply, have long been known to be specific to exercise modality [138, 139]. Strømme *et al*. [138] demonstrated that cyclists, cross-country skiers and rowers attained appreciably higher (4-14%) VO_{2max} values during exercise-specific test modalities than during treadmill running. In untrained individuals, VO_{2max} has been shown to be around 5% higher during ergometer rowing than treadmill running [52] which in turn yields values around 10% higher than ergometer cycling [140]. At submaximal intensities of exercise Hagerman *et al*. [139] showed that untrained participants achieve VO_2 values approximately 5% to 30% higher during ergometer rowing compared to cycling across a power output range of 50 to 250 W.

Several studies have indicated that anaerobic energy yield measured during exercise is also modality specific [140-144]. In exhausting exercise bouts lasting between 2.0 and 7.0 min, Bangsbo *et al*. [141] reported significantly higher (36%) anaerobic capacity values during ergometer rowing compared to treadmill running in rowers, concluding that active muscle mass, as dictated by exercise modality, influences anaerobic energy production. Similar conclusions were reached in studies which demonstrated appreciably larger (24-80%) absolute anaerobic energy yield during running at high (10-15% incline) versus low (1-5% incline) treadmill gradients [142-144]. More recently, anaerobic energy supply has been shown to be around 22% higher during exhaustive running versus cycling exercise lasting around 5.0 min [140]. According to Bundle & Weyand [76], the fact that maximum anaerobic attributable energy differs between modality and even within modality based on task specificity, implies that a single, whole-body anaerobic capacity during exercise does not exist for a given individual. Rather, the capacity for anaerobic energy supply appears to be limited by the demands imposed by the exercise modality and task since these determine the nature, magnitude and extent of muscle force production [76].

The vast majority of studies investigating energy system involvement or relative contribution during exercise have employed ergometer cycling or treadmill running [9]. In particular, early models of relative aerobic and anaerobic energy supply during maximum effort exercise [24, 85, 88, 89] appear to be based on studies which used these modalities only [38-40]. Given the potential of different exercise modalities to elicit different rates and yields of aerobic and anaerobic energy supply, it seems reasonable to question the generalization of relative energy system contribution from traditional models based on running and cycling to other exercise modalities.

2.1.4.6 Exercise Format

Within a given exercise modality, the format of an exercise bout largely dictates the pattern of intensity and duration during the bout and therefore influences the kinetics of ATP regeneration processes in skeletal muscle [118]. All-out effort and constant power output exercise are by far the most common formats imposed in studies assessing energy system involvement and relative contribution [9]. All-out effort exercise routinely elicits peak supramaximal power output within the first few seconds followed by an exponential decay to submaximal power output at task completion or exhaustion [76]. Fixed workload or constant power output exercise typically involves an arbitrary externally imposed supramaximal or submaximal power output maintained until exhaustion [145]. However, in competitive sport, most race events involve a constant work or fixed distance exercise format in which power output is planned and regulated—self-paced—based on individual exercise capacity in an attempt to complete a known exercise task in the shortest possible performance time [7, 63]. The exercise test format attempting to simulate these conditions is commonly referred to as a time trial [108]. The peak rate of anaerobic energy supply during all-out effort exercise has been shown to be more than double that elicited in a constant power output format [110], while VO_2 kinetics are faster in response to exercise initiated at a higher intensity [94] such as in all-out effort formats [110, 128]. The potential influence of exercise format on aerobic and anaerobic energy system response therefore warrants consideration when investigating relative energy system contributions during exercise.

Foley *et al*. [108] showed that total anaerobic energy yield during high intensity cycling bouts lasting 3.5 to 4.0 min was not significantly different between constant power output (110% VO_{2max}) and time trial (2.5 km) exercise formats. Gastin *et al*. [110] compared the mechanical work performed and energy system contribution during all-out effort (90 s) and constant power output (110% VO_{2max}) cycle ergometer exercise. Despite longer exercise durations (mean performance time = 208 s) in the constant power output format, total anaerobic attributable energy supply was not significantly different between exercise formats [110]. These results suggest that, for an exhausting exercise bout within a given exercise modality, a limited anaerobic capacity is available irrespective of whether an all-out effort, constant power output or time trial format is imposed, and exercise format is irrelevant in attempts at quantifying this capacity. However, management of the anaerobic capacity appears to be important in athlete pacing strategy during the completion of fixed distance or time trial exercise formats [146]. Foster *et al*. [135] showed that during self-paced time trial exercise (90 to 300 s bouts of ergometer cycling) power output is regulated in a pattern permitting conservation of some of the anaerobic capacity throughout an exercise bout. A centrally regulated pacing strategy is considered important in maximizing exercise performance, partly because this determines the manner in which the limited anaerobic capacity is distributed [109]. So while exercise format does not appear to alter total anaerobic energy supply measured during short- and intermediate duration maximum effort exercise, it does affect the rate and pattern of aerobic and anaerobic energy system involvement [110]. All-out effort and constant power output formats permit measurement of anaerobic capacity but fail to evaluate the manner in which this capacity is utilized in self-paced competitive events—an important indicator of athletic potential and successful sport performance [8, 109]. In addition, the proportional contribution represented by the anaerobic capacity to total energy expenditure during an exercise bout is dependent on the format of the exercise since absolute anaerobic energy yield is finite while total energy expenditure increases with exercise duration [63]. A fixed distance or time trial exercise format most closely mimics the performance demands of competitive sport events in terms of duration, intensity and pacing [8] and is therefore commonly recommended in the assessment of athletes [5].

2.1.4.7 Other Factors Influencing Energy System Contributions

During most voluntary, dynamic, whole-body exercise bouts the intensity, duration, modality and format of exercise largely dictate energy system involvement and relative contribution [9]. While specific investigations into the theme are limited in number, hypothetically, any of several other factors known or suspected to influence absolute VO_2 and/or skeletal muscle anaerobic ATP production could potentially influence proportional aerobic and anaerobic energy system contribution to total energy expenditure during an exercise task either independently or secondary to effects on exercise intensity and duration [26].

As with many physiological parameters, aerobic and anaerobic energy yield during a task is influenced by athlete morphology and body size [147]. Absolute aerobic energy supply as determined by VO_2 is significantly related to body mass at submaximal and maximum exercise intensity in untrained individuals and in highly trained athletes within several exercise modalities [147-150]. The capacity to supply ATP anaerobically is also dependent on the mass of exercising musculature [98] dictated not only by exercise modality [141] but also by body size and morphology [124, 133]. Additionally, while few studies have specifically addressed the theme, it appears that muscle fibre type composition is less important than active muscle mass in determining absolute anaerobic capacity during a given exercise task [141, 143]. Nevertheless, muscle fibre type composition differs between individuals and between skeletal muscles within the same individual [87] and may reasonably influence relative aerobic and anaerobic energy supply for a given individual [68].

Submaximal intensity endurance exercise training and high intensity speed or power exercise training are known to improve the absolute capacity for aerobic [104, 107, 111] and anaerobic [144, 151-154] energy supply respectively, but it is unclear to what extent training status alters proportional energy supply to total energy demand during an exercise task [153, 154]. Further, while absolute anaerobic capacity and VO_2 kinetics have consistently been shown to be different in athletes specifically trained for shorter, higher intensity compared to longer, lower intensity sport events within a given modality of exercise [84, 112, 124, 150, 155-157], this may not necessarily result in different relative energy system contributions during a maximum effort exercise task [150].

Compared to comfortable (e.g. 22°C, 50-60% relative humidity, RH) environmental conditions, hot (e.g. 29-33°C, 50-60% RH) conditions have been shown to elicit a proportionally higher anaerobic energy supply contribution during submaximal intensity exercise tasks in non-acclimatised individuals [158], and no difference in absolute anaerobic energy yield during supramaximal intensity exercise tasks in heat acclimatised athletes [159]. Reduced exercise performance and VO_2 kinetics during acute or chronic hypoxia, with [160, 161] or without [98, 162-166] changes in absolute anaerobic energy yield suggest that altitude has the potential to influence relative aerobic and anaerobic energy supply contributions during a given exercise task [24].

Habitual diet and acute nutritional status may affect exercise performance and relative energy system contribution secondary to altered skeletal muscle substrate availability and utilization [26, 78, 167] or dietary-induced pH changes [168, 169]. Prior exercise results in higher aerobic energy supply contributions to subsequent supramaximal intensity exercise, accounted for mostly by a higher VO_2 during early stages of the exercise bout with similar [170, 171] or lower [172, 173] total anaerobic energy supply. Some drugs may influence skeletal muscle aerobic and/or anaerobic energy supply during exercise by acting centrally to alter muscle fibre recruitment or peripherally to alter substrate mobilization [68]. Finally, absolute aerobic and anaerobic capacity is influenced by age and maturation status [174] and sex [140, 175], potentially influencing relative energy system contributions to a specific exercise task. It is likely that interactions occur between many of these factors during an acute bout of exercise, affecting the mechanisms regulating skeletal muscle aerobic and anaerobic energy supply during exercise [68].

2.1.4.8 Summary

Many factors act concurrently to determine the involvement and relative contribution of energy supply systems during exercise [26]. The ATP regenerated in skeletal muscle during maximum effort exercise bouts of short and long duration is proportionally dominated by anaerobic and aerobic energy provision respectively [9]. In athletes, maximum effort exercise performances lasting between 2.0 and 10.0 min elicit maximum absolute anaerobic energy yield irrespective of total work or mean power output [134]. A high rate of aerobic energy supply and optimal distribution of a large capacity for anaerobic energy supply are important for successful performance in events with durations in this range [135]. Aerobic and anaerobic energy system involvement and relative contribution is specific to the modality of exercise since this largely dictates the nature and extent of muscle contractile activity during an exercise task [25]. Most athletic events are not all-out effort or constant power output tasks, and the energy system contributions measured during such exercise formats are likely to differ from those during real-world, fixed distance, self-paced competitive events [115]. To appropriately simulate the intensity and duration of an athletic event, studies which investigate energy system involvement and contribution should employ formats of exercise specific to the pacing strategy employed by athletes [108].

2.1.5 Summary

The energy demand associated with muscle contractile activity, as with most forms of biological work, is met through the exergonic hydrolysis of ATP [70]. Regeneration of ATP in skeletal muscle occurs through several mechanisms—aerobically through O_2-dependent mitochondrial oxidative phosphorylation and anaerobically through sarcoplasmic substrate phosphorylation associated with PC splitting and glycolysis [71]. These energy supply systems have been well studied *in vitro* to elucidate the substrates and products involved, but knowledge about regulatory mechanisms limiting skeletal muscle ATP regeneration during voluntary exercise is still incomplete [21]. The instantaneous, periodic and cumulative energy system involvement and relative contribution during an acute bout of dynamic, whole-body exercise is largely a combined result of the intensity, duration, modality and format of the exercise [9] but is likely influenced by body size, muscle fibre type composition, training status and event speciality, environmental conditions, diet and nutritional status, and pharmacological agents [68, 112, 124, 156]. Skeletal muscle and/or whole-body aerobic and anaerobic energy supply is mediated through several intra- and extracellular regulatory mechanisms which act congruently in response to changes in ATP utilization associated with contractile activity during exercise and elicit an interdependent involvement of all ATP regeneration mechanisms [74].

Most investigations of energy system involvement and relative contribution during exercise have employed short duration cycling or running exercise in all-out effort or constant power output formats [9]. Consequently, there remains a comparative scarcity of empirical information regarding proportional aerobic and anaerobic energy supply during maximum effort exercise involving other exercise modalities, formats more representative of competitive sport events, and performance durations between approximately 2.0 and 10.0 min—exercise in which both aerobic and anaerobic energy supply mechanisms are heavily taxed [63]. Initial studies [38-40] and models [88, 89] of relative aerobic and anaerobic energy supply during exercise may have served as templates for models popularized by exercise physiology texts in subsequent decades [16, 19]. Few contemporary models [9, 68, 72] reflect the results of continued research in this theme subsequent to the earliest studies. Some of the disparity in results between initial and more recent investigations is likely due to varied measurement techniques, not all of which provide valid estimations of energy system involvement [9]. According to Hill [125] there are often misconceptions regarding the methods used to calculate aerobic and anaerobic energy system contributions during exercise, a theme addressed in the following section.

2.2 Assessing Energy System Involvement and Relative Contribution

2.2.1 Background

The capacity to perform endurance, strength or speed elements in athletic events can be measured in isolation fairly easily in contemporary exercise testing settings using an array of direct or indirect assessments [104, 111, 176, 177]. A plethora of procedural guidelines and normative data is available for measuring and interpreting parameters such as VO_{2max}, lactate threshold, anaerobic work capacity or peak power output in athletes participating in a variety of sports [178-180]. By contrast, far fewer measurements of aerobic and anaerobic energy supply during the performance of discrete sport events or event-specific simulations have been made [63], with the procedures involved largely remaining research tools for classifying sport demands rather than assessing individual physiological profiles [181]. While the magnitude of separate aerobic and anaerobic capacities may be important, the degree and pattern of use of these capacities during athletic performance is arguably more relevant when investigating sport-specific demands and individual athletic performance profiles [63]. This section reviews measurement techniques that have been employed to quantify aerobic and anaerobic energy system involvement and contribution during exercise tasks, with detailed attention to the theory and practice underlying the accumulated O_2 deficit technique.

2.2.2 Measuring Aerobic and Anaerobic Energy Supply

Attempts at quantifying the involvement and relative contribution of energy supply systems during exercise were first documented in the scientific literature over fifty years ago. Åstrand *et* *al*. [38] and Åstrand & Saltin [39] estimated aerobic and anaerobic energy supply during maximum effort cycle ergometer exercise bouts ranging in duration from 10 to 120 s using VO_2, O_2 deficit and an assumed mechanical efficiency. Fox *et al*. [40] used O_2 debt and blood lactate concentration following exercise to estimate relative energy system contribution during continuous and interval running. Understandably, experimental procedures have varied with time since these early investigations and have ranged from analysis of isolated skeletal muscle fibre preparations to measurements during dynamic whole-body exercise, with the results of the different approaches not being easily comparable [65].

The gold standard for measuring energy expenditure is heat loss measured by direct calorimetry [74]. This has been largely replaced by the more practical principle of indirect calorimetry—the measurement of O_2 utilization to estimate energy expenditure [80]. Whole-body aerobic ATP supply is directly related to VO_2 since aerobic ATP yield is necessarily O_2 dependent [24]. The VO_2 measured during rest or exercise provides a valid and reliable quantification of aerobic energy yield [24] and it has been used extensively for this purpose for decades [9, 84, 85]. The measurement of VO_2 using open-circuit spirometry is relatively simple in modern exercise testing laboratories, making the energy contribution associated with aerobic metabolism readily quantifiable [25]. Contemporary automated gas analysers with high data processing power permit the accurate and precise measurement of VO_2 and by implication, whole-body aerobic energy supply rate [25, 104].

Using VO_2 to represent total energy expenditure, or ATP turnover, is appropriate during steady-state exercise, but it underestimates energy expenditure during high intensity, short duration, or non-steady-state exercise, when anaerobic ATP supply significantly contributes to skeletal muscle energy demand [74]. In comparison to aerobic energy supply, determining the energy contribution from anaerobic mechanisms during exercise is more difficult and less precise [24]. Nevertheless, recognition of the importance of anaerobic ATP supply during many exercise and sport activities has led to considerable research effort in attempt to quantify it [115]. Direct approaches have measured biochemical changes in the concentrations of substrate molecules and derivatives in skeletal muscle [82]. Indirect approaches have inferred anaerobic energy system contribution based on measures such as mechanical power output during ergometer tests, post-exercise measurement of VO_2 and blood lactate concentration, or the O_2 deficit [26].

2.2.3 Muscle Biopsy

Changes in phosphagenic and glycolytic substrate and metabolite concentrations occur in skeletal muscle during exercise [182]. Biopsy immediately pre- and post-exercise permits direct assessment of anaerobic ATP supply associated with contractile activity in the section of sampled skeletal muscle [9]. Many studies evaluating methods for determining anaerobic energy yield have successfully used the muscle biopsy method [73, 119, 132, 183, 184] and it is considered the standard against which indirect measures should be compared [26].

While direct measurement of the change in concentrations of muscle ATP, PC, pyruvate and lactate is possible, it is of little practical value in quantifying total anaerobic energy system contribution during dynamic exercise owing to several limitations when estimating whole-body anaerobic energy release [26]. Firstly, the time delay between exercise termination and biopsy sampling, freezing and analysis may produce intracellular changes in substrate and metabolite concentrations, potentially confounding results [82]. Secondly, not accounting for lactate already released into the blood may result in the biopsy method underestimating anaerobic ATP yield [184]. Thirdly, the biopsy sample concentrations of substrates and metabolites have questionable representation of total muscle engaged in the exercise task [15]. Fourthly, totalling anaerobic energy supply using this method still relies on estimations of the active muscle mass involved in dynamic, whole-body exercise, which likely varies substantially between individuals and across exercise modalities [82]. Finally, while biopsy has long been used to provide direct measures of skeletal muscle biochemistry [113], the invasive nature of the technique generally renders it impractical for determining the energy produced via anaerobic metabolism during dynamic, whole-body exercise in elite athletes [26].

2.2.4 Magnetic Resonance Imaging

The principles of magnetic resonance imaging (MRI) were published by Lauterbur [185] and applied to studying skeletal muscle metabolic changes over forty years ago [186]. The nuclei of elements with uneven numbers of nuclear particles are magnetic such that atoms of naturally occurring non-radioactive isotopes (e.g. ^{31}P, ^{13}C, ^{1}H) already present in, or infused into an organism, become uniformly aligned on exposure to a powerful magnetic field [18]. Systematic application of rapid pulses of radio frequency magnetic fields superimposed on a fixed magnetic field causes molecules to resonate alternately between directions, a phenomenon detectable by sensitive scanners [22]. Identifying the spectrum of resonance patterns produced by different chemical nuclei allow the nature of compounds and their concentrations to be determined—

hence the term nuclear magnetic resonance (NMR) spectroscopy [18]. Determining the concentrations of compounds such as ATP, PC, P_i, H^+, water, fat and glycogen permit information on the biochemistry of imaged tissue to be obtained non-invasively [22]. The internal structure and function of living organisms is now commonly studied in biological research or medical practice using MRI techniques [187].

The potential application of such technology in exercise physiology is clear. Suggestions were that it would render biopsy procedures obsolete for the measurement of compounds localized in skeletal muscle while providing a larger, more representative sample, allowing a fair assessment of *in vivo* conditions [188]. However, concerns regarding the validity and reliability of some NMR spectroscopy measurements and associated calculations remain [111]. Also, while MRI facilities are available at most major medical centres, cost and practical utility have largely prevented their extensive use in measuring exercise-induced changes outside of research or diagnostic programmes [187]. Additionally, since MRI data acquisition requires motionless conditions it is currently restricted to studying skeletal muscle bioenergetics during restricted isometric or electrically stimulated muscle actions, or by comparing results before and after dynamic exercise [111].

2.2.5 Blood Lactate Concentration

Being simpler to measure and minimally invasive [145], the peak blood lactate concentration following exercise has long been used to estimate anaerobic energy supply [65, 100, 189-191]. A product of glycolysis [22], lactate partly distributes into interstitial fluid and blood [98] and its elevated concentration after high intensity exercise underscores the importance of skeletal muscle glycolytic activity for ATP regeneration during such exercise [192]. Lacour *et al*. [193] found significant correlations between blood lactate concentration and average running velocity over distances of 400 m (r = 0.89) and 800 m (r = 0.71), events in which anaerobic energy supply contributes significantly [194]. Further, sprint- and power-trained athletes, considered as having well-developed skeletal muscle anaerobic ATP supply mechanisms [156], typically attain higher post-exercise peak blood lactate concentrations than endurance-trained athletes and non-athletes [195]. The widespread use of blood lactate concentration as a measure of anaerobic capacity therefore appears understandable [115].

Lactate efflux from skeletal muscle fibres to interstitial fluid and blood takes time, introducing a temporal uncertainty regarding blood lactate measurements made during or after exercise [85].

The volume into which lactate molecules are released from skeletal muscle and therefore diluted in, is not easy to determine, and may represent as little as 6.0 L for blood or as high as 30.0 L for total body fluid in an average-sized male, which influences the estimations of glycolytic ATP regeneration [196]. Acute and long-term exercise-induced changes in blood volume further confound the use of blood lactate concentration in quantifying anaerobic energy yield [115]. In addition, some lactate reaching the blood already gets metabolised before sampling occurs [197]. Using the concentration of lactate in blood to estimate anaerobic energy turnover does not account for this uptake by less active muscle and other tissue [26]. Furthermore, quantifying blood lactate kinetics alone does not account for the anaerobic ATP contribution from intramuscular phosphagen sources [65], which may produce significant underestimations of anaerobic energy yield during short duration high intensity exercise tasks [9].

Recently published work [192] using mathematical modelling demonstrated that net lactate accumulation following high intensity rowing exercise rather than absolute concentration is significantly related to anaerobic energy supply as estimated with the accumulated O_2 deficit. However, these investigators obtained serial blood lactate measurements for over an hour post-exercise [192], limiting the practical utility of the method in routine exercise testing. The rate of whole-body lactate production cannot be measured directly in exercising humans, and since the blood concentration only reflects the dynamic balance between production and removal [197], blood lactate concentration has long been considered an unreliable estimation of muscle lactate production [24]. At best, blood lactate concentration may reflect the extent of stimulation of glycolysis [85], but it is not a valid quantitative measure of anaerobic energy supply during an exercise task [26, 74, 115].

2.2.6 Oxygen Utilization during Recovery from Exercise

The O_2 debt traditionally refers to the volume of O_2 utilized in excess of resting requirements during the recovery period following exercise [26]. Originally, theories described the O_2 debt as the O_2 utilized in metabolising lactate produced as a result of glycolysis during a preceding exercise bout [93]. Early research work demonstrating that PC regeneration is reliant on aerobic ATP supply following exercise [198] and that changes in VO_2 and blood lactate concentration follow similar time courses during recovery from exercise [189] provided impetus for the use of the O_2 debt in quantifying anaerobic energy yield during the preceding exercise [113, 190].

It has been recognized for some time that the energy equivalent represented by the O_2 debt is far greater than the anaerobic energy yield during a preceding exercise task [73] owing to an augmented ATP demand remaining after exercise which continues to be met via elevated oxidative phosphorylation [199]. The bulk of this elevated albeit declining demand for ATP is a result of residual elevated cardiac and respiratory muscle activity, stimulatory effects of elevated core body temperature and catecholamine concentrations, lactate gluconeogenesis, restoration of pre-exercise substrate and ion concentrations in muscle, and elevated post-exercise protein turnover [26, 73, 200]. A portion of VO_2 immediately following exercise is accounted for by replenishment of haemoglobin and myoglobin O_2 stores [113]. In acknowledgement that VO_2 following exercise does not represent the repayment of an initial anaerobic energy debt the term excess post-exercise O_2 consumption (EPOC) was preferentially advanced by Gaesser & Brooks [199]. Incidentally, the duration of O_2 debt measurement during recovery from exercise has not been standardized, ranging from 20.0 to 60.0 min [30, 40, 201], with suggestions that it may take 60.0 min or more for VO_2 to return to pre-exercise values [60]. Despite use in early attempts to classify exercise tasks based on reliance on anaerobic energy supply [40] and while still useful in quantifying the total energy cost elicited by an exercise bout [74], the use of post-exercise VO_2 to quantify anaerobic energy supply was discredited more than fifty years ago [113].

2.2.7 Ergometer and Field Test Performance

The external mechanical work performed or the power output maintained during field tests designed around a predetermined exercise duration and/or intensity remain extensively used as an index of power and/or capacity of the energy supply systems [145]. Tests are generally administered to maximize the contribution of a particular energy system based on theoretical models of proportional aerobic and anaerobic energy supply during maximum effort exercise of various durations [26]. Short duration high intensity exercise provides the circumstances in which aerobic energy supply, while not negligible [202], is generally considered the minor contributor for practical purposes [145]. Tests traditionally recommended include short duration jumping, staircase running, sprint running or cycle ergometer tasks [177, 203]. These tests may be useful in providing feasible, non-invasive indices of the peak rate of muscular power developed, or the amount of muscular work accomplished during brief periods of high intensity exercise [145]—considered a work estimate of the anaerobic capacity [115]. Tests lasting less than 10 to 15 s have been suggested as evaluating phosphagenic anaerobic capacity while those lasting 30 to 90 s have been considered as indicators of glycolytic anaerobic capacity [203].

Whether the results of these tests are useful in quantifying anaerobic energy supply is debatable [177]. There are at least three limitations when using performance in ergometer or field tests as a surrogate for assessing anaerobic energy system involvement, contribution or capacity. Firstly, oxidative phosphorylation is stimulated sufficiently in maximum effort exercise of short duration such that aerobic ATP supply during a 30 to 45 s test may represent as much as 20% to 40% of energy supply [119, 126, 202]. Secondly, evidence suggests that skeletal muscle glycolysis is significantly stimulated during maximum exercise as brief as 5 to 10 s, making it impossible to distinguish phosphogenic and glycolytic contributions from the power output maintained during short duration tests of this nature [90, 127]. Thirdly, as Serresse *et al*. [97] and Withers *et al*. [119] have shown, high intensity ergometer tests of short duration (10 to 30 s) are not able to fully exhaust anaerobic ATP supply capability and are therefore not suitable for quantifying the anaerobic capacity. Ultimately, the value of these tests is limited to providing a suggestion of high intensity work capacity in a particular exercise modality and format [204], since peak and average power output during these exercise tasks is a unique and complex product of muscle size, strength, contraction speed, fibre type composition, recruitment and coordination patterns rather than simply a reflection of phosphagenic and glycolytic ATP supply capability [145, 177].

2.2.8 Accumulated Oxygen Deficit

2.2.8.1 Background

Techniques for directly measuring total anaerobic energy contribution during dynamic, whole-body exercise are not currently available [23]. The most common method of inference of anaerobic energy yield during exercise has been through measuring the O_2 deficit, a concept introduced as early as 1920 by Krogh & Lindhard [205]. These exercise physiology pioneers had already recognized that VO_2 increases rapidly but not instantaneously during the transition from rest to exercise [206] and that this represents a period of augmented skeletal muscle anaerobic energy supply, labelling this temporary insufficiency in VO_2 the O_2 deficit [205]. By 1970 the O_2 deficit was accepted as a valid representation of an initial, transient anaerobic contribution to total energy supply during a bout of submaximal intensity exercise [200]. Hermansen [113] and Karlsson & colleagues [134, 163, 207] popularized the concept and appear to have published the first reports suggesting that the size of the O_2 deficit may indicate the average rate of anaerobic ATP supply during high intensity, non-steady-state formats of exercise. Medbø & colleagues [84, 98, 126, 132, 144] thoroughly revised the methodology for measuring the O_2 deficit and presented it as a means for measuring the maximum anaerobic capacity and quantifying the anaerobic energy yield during exercise tasks. The accumulated O_2 deficit (AOD) method has been used to report the proportional anaerobic energy contribution in an array of exercise modalities including running [63, 120, 194, 208], cycling [114, 124, 133], cross-country skiing [136, 150], swimming [114, 209, 210], kayaking [114, 123] and rowing [32, 35-37]. Formats of exercise as diverse as all-out effort isokinetic ergometer cycling [110], interval swimming with different rest periods [211], laboratory ramp test protocols [212], resistance training [213] and sprint hurdling [214] have been studied using the AOD method to quantify anaerobic energy yield. According to Gastin [26], widespread use of the AOD method is likely the result of its non-invasive approach to assessing the elusive anaerobic energy contribution during high intensity exercise. Key elements of this approach will be reviewed.

2.2.8.2 Fundamental Principles

A central principle of the AOD method is that since the power output achieved during exercise frequently demands ATP at a rate exceeding the momentary or maximum achievable rate through aerobic ATP supply [215], the difference is made up by anaerobic energy supply [77]. During maximum effort exercise the AOD is calculated as the difference between the estimated total equivalent O_2 demand of a task and the accumulated O_2 uptake measured over the duration of that same exercise task [98], expressed in equivalent units of O_2 and reported in absolute (L O_2 eq) or relative (ml O_2 eq$\cdot$kg^{-1}) terms [215]. The magnitude of the AOD therefore represents the ATP supply through means other than those accounted for by VO_2 during the time period of its measurement [65].

Contemporary open-circuit spirometry measurement apparatus permit simple and precise measurement of VO_2 during exercise and the AOD method takes advantage of this [216]. For a given submaximal intensity of exercise, steady-state VO_2 is assumed to reflect total energy turnover [24, 200]. The relationship between steady-state VO_2 and exercise intensity is termed the VO_2-power output (VO_2-PO) relationship and it appears to be linear throughout a range of exercise intensities [98]. Use of the AOD method assumes that a series of submaximal intensity exercise bouts can be used to establish the VO_2-PO relationship and that the resulting regression model can then be extrapolated to obtain the equivalent VO_2 demand associated with the power output achieved during a maximum effort exercise task [217], as illustrated in

Figure 2.2. Total equivalent O_2 demand represents the whole-body energy demand of an entire exercise bout and is a product of the equivalent VO_2 demand and the duration of the exercise bout [23]. Energy system contributions during an exercise task can then be calculated using the total equivalent O_2 demand and the accumulated O_2 uptake measured during the task [27]. The latter represents whole-body energy supply from oxidative phosphorylation during the period of measurement and includes the VO_2 associated with both resting and exercise-induced aerobic energy supply [216]. Describing the aerobic and anaerobic energy supply elicited by exercise requires that total equivalent O_2 demand and accumulated O_2 uptake be corrected for resting VO_2 although all but a few investigators have reported gross energy system contributions during exercise using the AOD method [30, 35, 124].

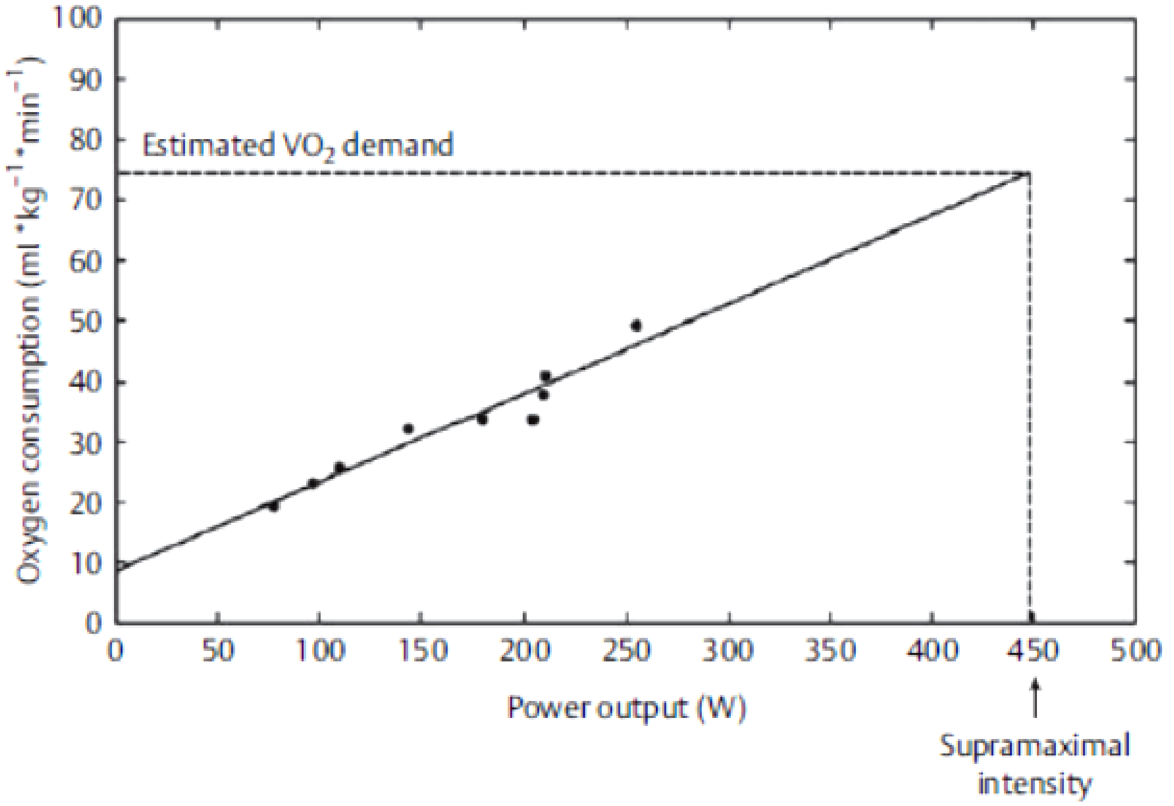

Figure 2.2: An individual oxygen uptake-power output relationship extrapolated to estimate the VO_2 demand associated with supramaximal intensity exercise.

Abbreviations: **VO_2** pulmonary oxygen uptake.

Note: Figure from Noordhof *et al*. [217].

Early investigations into the energy demand of high intensity exercise involved use of an assumed, common relationship between VO_2 and power output [134, 163, 201, 207, 218]. Employing a constant mechanical efficiency to estimate total energy demand is convenient, avoiding the need for additional exercise tests, but is of questionable validity [26]. Medbø *et al*. [98] demonstrated individual variations in the slope of the VO_2-PO relationship to be around 16% and so it is generally acknowledged that establishing and extrapolating individual mechanical efficiency using a series of submaximal intensity exercise bouts is important when using the AOD method [26]. The slope of the linear VO_2-PO relationship, the so-called delta efficiency, provides an index of individual mechanical efficiency within the exercise modality [98, 219-221].

Despite extensive use of the fundamental principles described above, no universal protocol has been accepted for determining the AOD [216]. The duration, number, intensity and format of the submaximal exercise bouts used in establishing individual VO_2-PO relationships have been the source of much variation and debate [184, 222-229]. In systematically redeveloping the major procedures of the AOD method Medbø *et al*. [98] used ten discontinuous 10.0 min treadmill runs at intensities between 35 and 100% VO_{2max} to establish the VO_2-PO regression models. Such a protocol imposes severe labour and time costs and has been acknowledged as impractical [26, 98], prompting investigators to study the effects of modified protocols.

In establishing the VO_2-PO relationship, shorter duration submaximal intensity exercise bouts typically yield lower VO_2 values for a given power output and may thus result in an underestimation of total equivalent O_2 demand and consequently AOD [98]. Changing the duration of submaximal intensity exercise bouts from 10.0 min to 4.0 min has been shown to result in 20% to 25% smaller AOD values [78, 224]. Other investigators have suggested that 4.0 min bouts are long enough to permit steady-state VO_2 to be achieved at submaximal exercise intensities but short enough to limit the size of the slow component during submaximal exercise intensities at or above anaerobic threshold [222], thereby preventing an overestimation of total equivalent O_2 demand and AOD [184, 219]. In practice, the duration of submaximal intensity exercise bouts used in the AOD method has varied from as short as 3.0 min [227] to as long as 7.0 min [225].

Buck & McNaughton [225] studied the effect of using different numbers and intensities of submaximal exercise bouts on the resultant VO_2-PO relationships. The differences were largest when the lowest and/or highest intensity exercise bouts were excluded from the analysis, but a reduced number of bouts spanning intensities from 40% to 70% VO_{2max} produced regression model characteristics similar to those obtained when ten bouts were used [225]. Reis *et al*. [229] showed that, in endurance-trained runners, including VO_2 values associated with submaximal exercise intensities above lactate threshold into the VO_2-PO regression equation did not produce significantly different AOD values, and cautioned that excluding such values may induce an underestimation of AOD. By contrast, Bickham *et al*. [223] suggested that including only data from below lactate threshold in a VO_2-PO regression model has the potential to significantly overestimate the O_2 demand of higher intensity exercise. According to Osborne & Minahan [216], in athletes, four to six exercise bouts spanning a range of intensities up to approximately 90% VO_{2max} are appropriate for developing an accurate VO_2-PO relationship, with recommendations that the analysis only include exercise intensities that yield steady-state VO_2 values.

The format of the exercise protocol used in establishing the VO_2-PO relationship has ranged from discontinuous bouts of submaximal intensity exercise separated by recovery periods lasting minutes [35, 141], hours [73] or days [32, 98, 156], to the submaximal intensity stages of standard incremental exercise tests [36, 123, 124, 161, 184, 230, 231]. Steady-state is generally elicited within the first four to six stages of an appropriately graded incremental exercise test but is dependent on the intensity of each stage relative to the exercise capacity of the individual [99]. According to Finn *et al*. [215], the most important criteria in establishing the VO_2-PO relationship appears to be that a steady-state VO_2 is present for all exercise intensities included in the regression model.

Characteristics of the maximum effort exercise performance to which the AOD method is applied have also received attention in the literature—most notably the modality and format of the exercise task. Firstly, the AOD appears to be highly task-specific. Bangsbo *et al*. [141] measured a 36% larger AOD in trained rowers during ergometer rowing compared to treadmill running. Both Olesen [142] and Medbø & Burgers [144] showed that high intensity treadmill running tests yielded larger AOD values when higher versus lower treadmill gradients were used. Craig *et al*. [124] demonstrated that sprint- and endurance-trained track cyclists attained maximum AOD measures when shorter (70 s) and longer (300 s) performance tests were used, respectively. Therefore the AOD, and consequently anaerobic energy supply, appears to be particular to the exercise modality, nature of the task and athlete training speciality [141]. Secondly, in efforts to measure maximal anaerobic energy yield, exercise intensities eliciting exhaustion within 2.0 to 5.0 min have traditionally been suggested since they are associated with the highest measured AOD values [98, 126, 131]. Such studies typically employ all-out effort exercise or constant power output tests to exhaustion [182]. The power output in all-out effort exercise formats begins well above VO_{2max} and decreases exponentially, introducing greater potential error in the linear extrapolation of submaximal intensity exercise efficiency to estimate total energy demand, and therefore AOD [15, 26, 232]. In addition, these formats of exercise present limitations when attempting to establish the energy system contributions to sport-specific events, which are typically not performed in an all-out effort manner, and which vary in duration based on the time to complete a given amount of work or distance [63, 115]. Although there is no difference between maximum AOD measured in constant power output tests to exhaustion and fixed distance protocols [108, 110], the time-course of anaerobic energy supply between these exercise formats is different [109]. Assessments of anaerobic energy yield in athletes by means of the AOD method should therefore incorporate sport-specific time trial or fixed distance exercise formats which best represent the demands of an athletic event, including the typical pacing strategy employed by athletes, and consequently the pattern of use of anaerobic energy supply [109, 115].

2.2.8.3 Validity

Since no direct measure of whole-body anaerobic energy supply exists against which to objectively compare results derived using the AOD method, most scientific debate has centred on the validity of its underlying theoretical principles [15, 78, 151, 233, 234]. The AOD method is based on two principle assumptions, namely, that total energy expenditure increases linearly with increasing exercise intensity, and that the energy demand of high intensity exercise is constant over time [98, 151, 235, 236]. These assumptions have been described as tenuous by some [115], with critics citing several observations in rejecting the validity of the AOD method for calculating anaerobic energy yield during maximum effort exercise.

Firstly, VO_2 at high but still submaximal exercise intensities has been found to be higher than expected based on linear extrapolations from lower intensities [99, 141], although not by all investigators [219, 235]. By implication, through heavy submaximal exercise intensities, the VO_2-PO relationship may not be linear [15, 141]. Secondly, during high but still submaximal intensity exercise, such as above anaerobic threshold [99], VO_2 is a function of time [102], and the rising slow component of VO_2 may prevent an accurate interpretation of energy expenditure during exercise at such intensities [103]. Thirdly, some anaerobic energy supply contributes to producing high but still submaximal intensity work rates, possibly representing as much as 10% of the aerobic energy supply [73]. This energy cost appears unaccounted for when using VO_2 to represent total energy demand and establishing the VO_2-PO relationship in the AOD method [15]. Fourthly, using O_2 equivalent units extrapolated from submaximal intensity steady-state VO_2 values to represent total energy demand assumes that aerobic and anaerobic energy supply are equally efficient [80]. Some [237] but not all [220] investigators have reported differences in the efficiency of aerobic and anaerobic ATP regeneration. Finally, high intensity exercise is characterized by progressive changes in body stabilization demands, cardiorespiratory work, core body temperature, catecholamine concentrations, substrate utilization and muscle contractile efficiency [26, 173, 220, 221]. Together, these observations suggest that, in comparison to submaximal intensity exercise, high intensity exercise is neither equally nor constantly efficient.

However, several lines of evidence support the validity of the AOD concept. Poole *et al*. [219] simultaneously measured both pulmonary VO_2 and O_2 utilization at an exercising leg during ergometer cycling over a range of submaximal exercise intensities approximating 20% to 90% VO_{2max} in an effort to determine whether changes in VO_2 reflect changes in O_2 utilization at skeletal muscle. These investigators found that while VO_2 measured at the mouth, reflective of whole-body O_2 utilization, was expectantly higher than O_2 utilization measured across one exercising leg, the slope of the relationship between exercise intensity and either pulmonary VO_2 or leg O_2 utilization was not significantly different [219]. Through a wide range of submaximal exercise intensities, the change in steady-state VO_2 therefore appears to accurately reflect the change in muscle O_2 utilization [98].

While Poole *et al*. [219] made all measures 3.0 to 5.0 min after the onset of exercise to limit the size of the slow component of VO_2, Whipp & Wasserman [99] demonstrated that well-trained participants are able to attain steady-state VO_2 values within 3.0 to 5.0 min even at high but still submaximal exercise intensities around anaerobic threshold, results since corroborated by Bickham *et al*. [222]. Further, Russell *et al*. [227] demonstrated that the magnitude of the slow component is considerably lower in endurance-trained athletes than in non-athletes. The results of these studies support contemporary recommendations for using the VO_2-PO relationship established from steady-state VO_2 values attained during submaximal intensity exercise bouts as a reasonable reflection of the change in O_2 utilization associated with a change in external power output in endurance-trained athletes [182, 215, 216].

The AOD may be relatively unaffected by any potential difference in efficiency between submaximal and high intensity of exercise [26]. Gastin *et al*. [110] showed that the AOD is not significantly different when supramaximal exercise is performed at different intensity (110% versus 125% VO_{2max}) or format (constant power output versus all-out effort), suggesting that the AOD is not greatly affected by possible differences in efficiency when using linear extrapolation methods. Since the decrease in mechanical efficiency with increasing intensity may be a progressive phenomenon throughout the exercise intensity range rather than a threshold occurrence [220], altered efficiency may automatically be integrated into the linear extrapolation of steady-state VO_2 data from multiple bouts of submaximal intensity exercise [9]. Indeed, the slope of the VO_2-PO regression line, the delta efficiency, reflects the mechanical efficiency of each additional increment in power output for a given exercise modality [219]. Every VO_2 value included in the regression analysis of the AOD method is a reflection of the change in O_2 demand associated with a given power output—a demand which includes the influence of a change in mechanical efficiency [110]. Including a wide range of exercise intensities in establishing the VO_2-PO relationship may therefore inherently include progressive changes in efficiency such that underestimation of the total energy demand associated with high intensity exercise is minimized [26, 222, 229].

Nevertheless, it has been acknowledged that the size of the AOD and therefore anaerobic energy supply is likely underestimated for very short duration high intensity exercise tasks [15, 232], with larger errors for exercise tasks in which power output far exceeds maximum aerobic power [151]. According to Reis *et al*. [229], the larger the difference in power output between the highest submaximal intensity bout used in establishing the VO_2-PO relationship and the supramaximal intensity exercise task being assessed, the larger the error in estimating total energy demand and thus AOD. This represents the central challenge to the validity of measuring AOD for determining anaerobic energy yield during short duration (less than approximately 120 s) high intensity (greater than approximately 120% VO_{2max}) [9]. However, for longer duration (longer than approximately 120 s) submaximal intensity or maximum effort exercise in which the power output achieved more closely approximates those used in establishing submaximal exercise efficiency through the VO_2-PO relationship, the anaerobic energy supply can be accurately estimated by measuring AOD [73].

The validity of the AOD method is supported by investigations demonstrating its close relationship with anaerobic ATP yield determined through direct biochemical measures [26]. Bangsbo *et al*. [73] compared anaerobic energy supply as measured by AOD with biopsy-determined substrate and metabolite changes using a single leg exercise task. The results indicated no significant difference between the anaerobic energy yield measured using the two methods after correcting AOD for a decrease in peripheral O_2 stores, supporting the AOD technique as a measure of anaerobic energy supply in exercise involving a limited muscle mass [73]. Medbø *et al*. [98] reported that the AOD method produced an estimation of whole-body anaerobic capacity (72.0 ml O_2 eq·kg^{-1}) in agreement with predictions of theoretical maximum anaerobic energy release (66.0 ml O_2 eq·kg^{-1}) based on data in the literature on changes in ATP, PC and lactate concentrations and peripheral O_2 stores during high intensity exercise. Medbø & Tabata [132] reported a close relationship ($r = 0.94$) between indirectly assessed whole-body anaerobic energy release using the AOD method and direct measures of anaerobic energy turnover using biopsied muscle following exhaustive exercise. However, this investigation was criticised by Bangsbo [15, 151] for use of assumed values for active muscle mass, failure to account for lactate release into circulation and the wide range of exercise durations (30 to 180 s) used in establishing the correlation. Nevertheless, Withers *et al*. [119] also produced results supporting a close relationship between anaerobic energy supply determined by AOD and muscle biopsy methods during high intensity cycling exercise lasting 30 to 90 s. Conversely, Green *et al*. [184] reported no significant correlations between AOD and anaerobic ATP supply determined *in vitro* from muscle biopsy in trained cyclists, with the authors implicating error in one or both of the methods in interpreting the findings. Having made use of short duration high intensity exercise performance trials the authors speculated that use of a submaximal VO_2-PO relationship to predict supramaximal energy demand may well have exacerbated the error involved [184].

Beyond comparison with the results of direct methods, it is worth considering how AOD measures relate to other indirect, field techniques indicative of anaerobic work capacity, such as performance in short duration high intensity exercise tests [145]. In two of the earliest examples of such comparisons, both Lawson & Golding [201] and Szogy & Cherebetiu [204] reported that the O_2 deficit incurred during a 1.0 min cycle ergometer test correlated significantly with total work performed. Ramsbottom *et al*. [238] reported stronger correlations (r = 0.88 and 0.82) between shorter (100 and 400 m respectively) rather than longer (r = 0.61; 800 m) running performance and maximum AOD, a phenomenon demonstrated by several other studies [156, 201, 239]. Hill & Smith [240] compared anaerobic work capacity measured using a power-time model of ergometer performance with anaerobic capacity determined by maximum AOD during cycling and found significant correlations (r = 0.77) and no significant differences (p = 0.44) between the anaerobic energy yield the two methods returned. More recently, Bosquet *et al*. [241] confirmed these results in reporting significant correlations between AOD and estimated anaerobic running capacity based on field test performance. While the relationship between AOD and performance in short duration high intensity ergometer and field tests is not always high, it does suggest that common characteristics underlie both measures [26].

In short duration high intensity exercise tasks that are proportionally dominated by anaerobic energy supply, athletes specifically trained for strength, power or speed events tend to perform better than athletes trained for endurance events [195]. It may therefore be reasonably hypothesized that a valid measure of anaerobic energy supply should be able to differentiate between these categories of athletes [156]. Average AOD values for sprint-trained, middle-distance-trained and endurance-trained athletes approximate 80-85, 75 and 50-65 ml O_2 eq·kg^{-1} respectively [98, 144, 156]. Comparisons between groups based on event-specificity or sex have repeatedly yielded 15% to 36% larger maximum AOD values in sprint-trained athletes [84, 112, 124, 150, 155, 156] and approximately 30% higher values in males [140]. Scott *et al*. [156] demonstrated that higher maximum AOD values in sprint-trained athletes were linked to significantly greater anaerobic energy contribution (39% versus 30%) in an exhaustive run at 125% to 140% VO_{2max} compared to endurance-trained athletes. Beyond the results of these cross-sectional studies, the AOD appears to be responsive to high intensity activity-specific exercise training, improving by around 5% to 30% after intensified periods of training [144, 151-154].

A true anaerobic capacity should theoretically be described by the anaerobic energy supply during an exercise bout increasing until some practical limit is achieved, with the largest total supply being represented as the maximum AOD [98]. Karlsson & Saltin [134] demonstrated that despite different durations (2.0, 6.0 or 16.0 min), maximum effort exercise produced remarkably similar AOD values (4.9, 5.0 and 4.8 L O_2 eq respectively) irrespective of differences in mean exercise intensity or accumulated O_2 uptake between the bouts. Foster *et al*. [109] confirmed this phenomenon in reporting similar AOD values in self-paced maximum effort exercise tasks over different distances. The gravitation of O_2 deficit toward a maximum in exhaustive exercise despite different exercise durations is considered important in establishing the AOD as an appropriate measure of anaerobic energy supply [145].

Finally, Medbø *et al*. [98] and Linnarsson *et al*. [163] demonstrated that reducing inspired O_2 content produced no significant change in AOD magnitude despite reduced VO_2 and exercise power output. In repeated exercise bouts, acute hypoxia exposure has been shown to produce cumulative AOD measures no different to those obtained in normoxia [164]. Bro-Rasmussen *et al*. [160] reported similar increases in muscle buffer capacity (6-8%), treadmill running performance (11%) and O_2 deficit (12%) following a period of high altitude exposure while VO_{2max} remained unchanged. The fact that AOD appears independent of VO_{2max}, effectively discriminating between aerobic and anaerobic energy provision, is an important requirement for a measure of anaerobic energy provision [26] and provides support for the AOD method as a valid measure of anaerobic energy yield [98].

2.2.8.4 Reliability

Measures of AOD reliability are generally lower than those reported for mechanical power output or anaerobic work capacity using performance in short duration high intensity exercise tests [177]. Since the AOD is derived from multiple measures of submaximal intensity VO_2 and a maximum effort exercise performance, each with their own sources of error, the variability of O_2 deficit is always likely to be greater than that of isolated physiological (e.g. VO_{2max}) or performance (e.g. ergometer power output) measures [115]. Pate *et al*. [242] reported test-retest correlation coefficients (r = 0.73) for O_2 deficit suggestive of good reliability in exercise tests at an intensity of approximately 120% VO_{2max}. Using a similar intensity of exercise Graham & McLellan [243] studied the variability of O_2 deficit in trained cyclists, and reported relatively large individual coefficients of variation (8-13%) but no significant difference between repeated tests, concluding that the AOD method was a reliable technique for studying the metabolic changes in athletes. Withers *et al*. [119] reported test-retest correlation coefficients of 0.96, 0.95 and 0.84 for O_2 deficit measured during 30, 60 and 90 s of all-out effort cycling exercise respectively. Ramsbottom *et al*. [238] found good agreement (r = 0.94) and no significant difference between the O_2 deficit measured during successive inclined treadmill runs at 120% VO_{2max}. Jacobs *et al*. [244] reported a test-retest correlation coefficient of 0.97 and no significant differences for repeated AOD measures during exhaustive cycle ergometer exercise at 125%

VO_{2max}, while Weber & Schneider [245] concluded that the maximum AOD is a repeatable measure based on intra-class correlation coefficients of 0.95 and 0.97 for high intensity cycling at 110% and 120% VO_{2max} respectively, with no significant differences between values in consecutive tests. While these studies used either all-out effort or constant power output performance tests, Foster *et al*. [131] reported good agreement between the O_2 deficit measured in paired cycling trials over a fixed amount of work, concluding that the AOD was reproducible in a time trial format of exercise which demands a realistic and competitively familiar pacing pattern by athletes. These results were corroborated by Foley *et al*. [108] who demonstrated that the AOD was reproducible in both constant intensity (110% VO_{2max}) and constant work (2.5 km time trial) cycling performance tests, and therefore represents a reliable means of assessing anaerobic energy supply in athletes in competitive simulations.

The reliability of the AOD method is dependent on the precision of establishing the total equivalent O_2 demand of the maximum effort exercise task [226]. Since this must be extrapolated from the submaximal VO_2-PO relationship, even small errors in establishing this relationship can lead to significant error in calculating total equivalent O_2 demand and consequently, AOD. Bickham *et al*. [222] highlighted the need for accurate data collection during AOD procedures to minimize variability and a concomitant reduction in precision of the total equivalent O_2 demand estimation. In light of the assumptions and procedures involved in the AOD method, several considerations appear important in minimizing methodological sources of variability. In athletes, employing a wide range of exercise intensities to determine the associated VO_2, incorporating steady-state VO_2 values obtained over the same time period during submaximal intensity exercise bouts, and extrapolating individually determined submaximal VO_2-PO relationships to determine total equivalent O_2 demand in high intensity exercise have been suggested [98, 227, 229]. Laboratory and participant conditions need to be controlled and standardized as far as possible so as to make submaximal intensity VO_2 values as representative of energy demand as possible [115]. Carefully controlled conditions and procedures are essential since the VO_2 measured at a given exercise intensity is influenced by many factors such as prior exercise, recent dietary intake, mood state, time of day, environmental conditions and experience with the exercise modality [246].

The precision of the AOD method was initially expressed using only the interclass correlation coefficient of the VO_2-PO relationship with studies typically reporting r values exceeding 0.93 [32, 36, 114, 124, 133, 161]. However, given that a reduced number of points in the regression model still permits a high VO_2-PO correlation coefficient despite a reduction in the precision of measuring AOD [225], other indices of precision have been advocated. These include the standard error of the regression line (typically 4.0 to 6.0 $ml \cdot kg^{-1} \cdot min^{-1}$), the standard error of the estimated equivalent O_2 demand (typically 3.0 to 6.0 $ml \cdot kg^{-1} \cdot min^{-1}$), and/or the precision of the AOD estimate itself (typically 3.0 to 13.0 $ml \cdot kg^{-1}$ [98, 209, 210]. Other investigators have reported the width of the 95% confidence interval of the estimated equivalent O_2 demand obtained from linear extrapolation (typically 5.0 to 20.0 $ml \cdot kg^{-1} \cdot min^{-1}$) to indicate the precision of the method [152, 209, 210, 222, 226]. Some investigators have suggested the forced inclusion of a constant y-intercept value into the VO_2-PO regression equation to improve precision and therefore reliability of the AOD method [222, 227] although in practice this has only been done by a few investigators [35, 114, 222, 226]. Bickham *et al*. [222], in describing factors that may enhance the precision of the AOD method, suggested employing an even spread of submaximal exercise intensities above and below lactate threshold—including intensities closer to the intended forecast. Gastin [26] recommended that, at the very least, information concerning the VO_2-PO relationship and precision of estimating total energy demand should be reported in studies making use of the AOD method.

2.2.8.5 Aerobic Component of Oxygen Deficit

The AOD represents the energy supply derived largely, but not exclusively, from means other than oxidative phosphorylation [26]. Besides the anaerobic ATP yield from PC splitting and glycolysis, the AOD includes a small aerobic contribution to skeletal muscle ATP regeneration that is not accounted for by VO_2 measured between the start and end of an exercise bout [98]. A contribution to muscle energy supply from aerobic ATP regeneration is made following the initiation of exercise through use of O_2 already present in the lungs, bound to haemoglobin and myoglobin, and physically dissolved in peripheral body fluids [92]. This may represent the minor yet significant contribution to oxidative ATP regeneration during exercise [98], approximating 9% to 10% of total AOD during high intensity exercise [145, 216], prompting debate on its appropriate allocation into either the aerobic or anaerobic energy yield [133]. Accurately evaluating the size of endogenous O_2 stores in humans and degree of desaturation during dynamic, whole-body exercise remains problematic, and no direct technique is available [98]. This may explain why few investigators [84, 98, 126, 136, 150, 231, 247] appear to have considered it when reporting anaerobic energy supply using the AOD method. As early as 1920 Krogh & Lindhard [205] suggested that around 500 ml of the estimated 750 ml peripheral store of O_2 was utilized during the initiation of exercise, congruent with subsequent claims that 400 to

600 ml of the endogenous O_2 store forms part of the O_2 deficit measured during high intensity exercise [24, 60]. The argument has been made that any overestimation of AOD by ignoring the aerobic contribution from peripheral stores of O_2 might simply counter the potential underestimation of the AOD from ignoring the supposed lower mechanical efficiency of high intensity exercise when estimating its VO_2 demand from the submaximal VO_2-PO relationship [133]. Nevertheless, recent guidelines to exercise scientists are to subtract the energy contribution of this source from the AOD and add it to the accumulated O_2 uptake to provide a more accurate reflection of anaerobic and aerobic energy release respectively, and to report both the adjusted and unadjusted AOD values [145, 182, 216].

2.2.8.6 Current Consensus

The AOD method has become popular in applied exercise physiology and sport research settings for assessing the energy supply attributable to anaerobic mechanisms during maximum effort exercise [115]. It relies on extrapolation from the efficiency of submaximal intensity exercise to determine total energy demand during a supramaximal intensity of exercise which can then be divided into aerobic and anaerobic contributions using the VO_2 measured during the exercise task [98]. Debate over the validity of the AOD method and its underlying assumptions has resulted in criticism of its use in measuring the anaerobic energy supply during high intensity, dynamic, whole-body exercise [15]. While efficiency differences between submaximal and supramaximal intensity exercise may be unresolved [26], the error in calculating total energy demand and consequently anaerobic energy supply using the AOD method is larger for exercise tasks involving very high power output performed to exhaustion in an all-out effort format [151]. Definitively establishing the validity of the AOD method is complicated by the absence of a criterion gold standard for measuring anaerobic energy yield during whole-body exercise [115].

While acknowledging concerns regarding the AOD method in a recent review Noordhof *et al*. [27] described it as *"…reasonable from a conceptual standpoint…"* and "…*probably the best non-invasive method…*" for determining anaerobic energy supply. It appears that the benefits of using the AOD method outweigh the limitations [80] and it is therefore unsurprisingly the most extensively used method for estimating energy system contribution during high intensity exercise [9]. Use of the AOD method is considered valid for assessing anaerobic energy yield based on at least five lines of evidence in the research literature: 1. the quantitative similarity between anaerobic energy supply determined by the AOD method and skeletal muscle biochemical measurements; 2. the good correlation between AOD and performance in short duration high intensity exercise tasks; 3. the larger AOD achieved by sprint-trained as opposed to endurance-trained athletes and non-athletes; 4. the increase in AOD that has been shown following high intensity training interventions; and 5. the ability of the AOD method to discriminate between aerobic and anaerobic energy yields. The maximum AOD attained during exercise is considered a valid and reliable measure of anaerobic capacity within an exercise modality [26, 27, 98, 245], supporting the strong theoretical foundation of the AOD as a measure of anaerobic attributable energy supply [26].

When its assumptions and methodological concerns are understood and acknowledged the AOD remains the best practical method for determining anaerobic energy supply in elite athletes performing dynamic, whole-body exercise tasks [27]. However, studies using the AOD method display inconsistencies in procedures and calculations which have potentially restricted its practical utility for sport science practitioners. Specifically, the minority of investigators appear to correct measures for resting VO_2 and report net aerobic and anaerobic energy contributions during an exercise task [30, 35, 124]. Likewise, few investigators have corrected AOD measures for the use of peripheral O_2 stores [84, 98, 126, 231, 247]. These are important considerations in accurately reporting the energy cost and relative energy system contributions during exercise activities and warrant attention in investigations making use of the AOD method.

2.2.9 Summary

Unlike aerobic energy supply, quantifying anaerobic energy supply cannot be done simply [23] and while a variety of techniques have been used in attempting it, there remains no universally accepted method for measuring anaerobic energy turnover during whole-body exercise [177]. Further, since there is no direct method for measuring whole-body anaerobic energy supply, the estimations from the various techniques cannot be properly validated [9]. All methods employed to date have advantages and disadvantages and while some may result in similar estimates of anaerobic energy turnover under some conditions, different methods should not be used interchangeably [23]. Most early investigations into the relative aerobic and anaerobic energy supply during exercise employed methods which are now less favoured as a result of known inaccuracies [9].

Advancing the understanding of the demands of a competitive sport event through studying and reporting aerobic and anaerobic energy system contributions necessitates, among other things, employing an analysis technique which appropriately differentiates the energy supply mechanisms supporting dynamic, whole-body exercise [15]. The most accepted, used and recommended measure of anaerobic attributable energy supply during sport-specific exercise is the AOD [27] and it is likely that this will remain the case until alternative methods involving modern technologies become suitable for measurements during dynamic, whole-body exercise in humans [60]. If the proportions of aerobic and anaerobic energy supply are assessed in athletes using the accumulated O_2 uptake and AOD respectively, then measurements should be made under exercise conditions specific to the competitive event [115]. Since the AOD and anaerobic energy supply have been demonstrated to be highly specific to an exercise task [141, 142, 144] and athlete training speciality [124], it is important that relative energy system contributions to a sport event not be generalized from studies involving other athletes or exercise modalities simply on the basis of similar performance duration [115].

2.3 Applied Physiology of Rowing

2.3.1 Background

Rowing developed in antiquity to traverse large bodies of water before feasible over-land networks were extensively developed [248]. As a sport, rowing was established in the eighteenth century in England—due largely to the initiative of professional ferrymen—and institutionalized in the nineteenth century by amateur university rowers [249]. Rowing is one of only five sports that have appeared at every modern Olympic Games since the first edition in 1896 [250]. It has the third largest quota of athletes per sport at the Olympic Games after athletics and swimming, with over 500 competitors and fourteen sets of rowing medals on offer [251]. Several variations of the sport have developed, including indoor ergometer rowing and coastal or oceanic rowing [248].

In the nineteenth century scientific inquiry in rowing centred mostly around equipment design [250] although descriptions of technique, training and physiological responses to rowing from the period are available [252]. The past fifty years however, has seen an acceleration in scientific investigation into the sport and its participants (oarsmen and oarswomen), yielding a significant volume of research on the biomechanics, physiology, anthropometry, injury and illness, nutrition, performance analysis and training of rowers, with several extensive scientific reviews of these aspects of the sport available [4, 10, 12, 13, 253-255]. This section presents a review of literature supporting an understanding of exercise metabolism in elite rowers during competitive or simulated rowing races. Attention is given to competitive rowing performance, physical and physiological characteristics influencing rowing performance, rowing ergometry for the scientific and performance assessment of rowers, physiological demands of rowing, and the exercise metabolism associated with rowing and rowing ergometry.

2.3.2 Fundamental Characteristics of Rowing

Rowing involves competitors traveling backwards on a water course in vessels propelled by oars, principally using the force generated by the muscles of the legs, back and arms [251]. Competitive rowing races are held over a race distance of 2000 m on purpose-built courses [34]. Rowing competitive categories are divided by sex, weight class (lightweight or heavyweight), number of rowers in the boat (1, 2, 4 or 8), the presence or absence of a coxswain, and into sculling or sweep-oar rowing [10]. Unique to rowing among forms of dynamic human exercise or locomotion is that the body mass is supported in a seated position while both legs are involved in producing force simultaneously during the rowing action, or stroke [254]. Each rowing stroke is divided into two phases which are repeated in cyclic fashion [10]. The drive phase involves force production by a large proportion of skeletal muscle mass and is alternated with the slightly longer recovery phase in which body position is actively prepared for the next stroke [256]. The rowing movements are performed on a sliding seat in a rowing boat, or shell, such that the drive phase and resultant acceleration of the boat is achieved by the sequential but non-distinct extension of the legs and trunk, and flexion of the arms [13]. The leg drive (40-50%), trunk extension (40-50%) and arm pull (10-20%) are the major producers of force during rowing [257] although these relative contributions are dependent on stroke rate, athlete morphology and rowing technique [258]. To overcome the high resistance of a water environment successful rowing performance relies heavily on the ability to produce and convert muscular force into boat velocity through the use of the oars [13]. These requirements are fundamentally different to those faced by other endurance-trained athletes such as runners or cyclists in overcoming the lower forces of air resistance and surface friction [10, 65, 253].

2.3.3 Rowing Performance

The outcome of a standard competitive rowing race is decided among a group of boats competing together but in separate lanes on a water course, and is based on the shortest time taken to complete the 2000 m distance [10]. Performance time, or highest mean velocity, is therefore the decisive performance variable in competitive rowing [259]. Depending on competitive category, boat class, and weather and water conditions, rowing races generally last between 5.5 and 7.5 min [28]. According to Volianitis & Secher [248], across the various rowing events, performance time improved by an average of 0.7 s per year over the 2000 m race distance since 1900, although such analyses are confounded by differences in regatta weather and water conditions which significantly affect boat velocity [258].

Improvements in performance during the early years of competitive rowing were rapid and almost certainly due to significant developments in rowing equipment before the standardization of rules governing technology tempered performance improvement [34]. Additionally, Volianitis & Secher [248] suggest that training methods may have approached a limit in biological or logistical terms, and stricter doping control procedures may have been instituted in more recent times, contributing to slower improvement in international rowing performance. Nevertheless, Seiler [260] identified several factors likely contributing to the small but ongoing performance improvement in international rowing. These include: the availability and selection pressure into rowing of individuals with larger physical and physiological capacities; the essentially professional sporting life and consequently improved preparation of rowers in many developed countries; and improved training for rowing-specific demands [260]. As far as the latter is concerned, recent decades have seen the widespread involvement of scientific and medical support in the preparation of rowers, better educated and more experienced full-time coaches, refinement of rowing technique, and more time spent training [34]. In particular, extensive use of indoor rowing ergometers has meant greater amounts of physical and technical preparation are possible, with training time lost as a result of poor weather largely a thing of the past [10].

2.3.4 Rower Characteristics Related to Successful Performance

Rowing performance is influenced by the power output generated by the rower(s), the efficient and effective utilization of that power output to attain and sustain high boat velocity, and the forces resisting boat progression [261]. The last of these, the external mechanical energy cost, is relatively uncontrollable, being a product of equipment regulations and environmental conditions [10], but the first two factors are influenced by characteristics of the rower(s) [253]. The physical and physiological characteristics most frequently demonstrated to be significantly related to rowing performance are summarized in this section. It is acknowledged that mechanical, psychological, technical, tactical and environmental aspects [4] beyond the scope of this study also contribute significantly to rowing performance and competitive outcome.

Most [12, 35, 41, 44, 45, 55] but not all [262, 263] studies which measured rower anthropometric characteristics have revealed that body mass and stature are related to rowing performance within groups of experienced rowers and across a variety of competitive categories. Successful rowers are reported to have long limbs, not only in absolute terms, but also relative to their stature [42]. While more accomplished rowers are typically taller and heavier than less accomplished counterparts [264] they also tend to be leaner [10], with lower subcutaneous skinfold thickness values and body fat content [28]. Lightweight rowers in particular tend to be exceptionally lean athletes, with estimated body fat representing approximately 7% and 15% of body mass in male and female lightweight rowers respectively [10]. Strong relationships between muscle mass and both ergometer and on-water rowing performance times have been demonstrated [43, 45, 263]. These physique characteristics likely permit the transfer of large muscular forces into biomechanically effective rowing movements while minimizing the energy cost associated with moving the body [265], and other than the low body fat content, are unique among endurance-trained athletes [264].

Rowing performance in both on-water and ergometer modalities has consistently been shown to correlate highly with VO_{2max} [35, 36, 41, 43, 45, 47, 50, 51, 53, 55, 56]. Secher *et al*. [41] reported a significant relationship between final placing at an international regatta and mean VO_{2max} of the rowing crew expressed in absolute ($r = 0.87$) but not relative ($r = 0.38$) terms. It has long been evident that across different sports, elite rowers attain absolute VO_{2max} values among the highest recorded [4], with values of 6.0 to 6.6 $L \cdot min^{-1}$ being routinely measured for heavyweight men—largely a reflection of the larger body size of rowers compared to other endurance-trained athletes [10]. Relative to body mass, VO_{2max} values of 65 to 75 $ml \cdot kg^{-1} \cdot min^{-1}$ are typically reported for elite rowers [41, 266]. Superior rowing performance has also been linked to a faster VO_2 response at the initiation of exercise [55] and the ability to achieve and sustain a higher VO_2 during simulated racing [46]. Maximum aerobic power is higher in more successful compared to less successful rowers [43]. Indeed, peak power output during incremental rowing ergometer testing has been shown to be a strong predictor of 2000 m ergometer performance [53]. This evidence supports the contention that successful rowers are able to achieve high rates of aerobic energy supply [12].

At submaximal exercise intensity, the ability to sustain a high percentage of VO_{2max} for prolonged periods of time and a high rowing efficiency have been associated with superior rowing performance [12]. The economy of movement has been suggested as an important physiological and biomechanical determinant of rowing success [51], although there is evidence both for [46] and against [35] a significant relationship between mechanical efficiency and rowing performance. Bourdin *et al*. [53] found statistically significant but not strong correlations between rowing performance and both gross rowing efficiency (r = 0.35) and VO_2 at anaerobic threshold (r = 0.49). Ingham *et al*. [51] reported a strong correlation between 2000 m rowing ergometer performance and VO_2 at lactate threshold, findings corroborated by Cosgrove *et al*. [43] and Riechman *et al*. [263]. Better rowing ergometer performance has also been associated with improved lactate exchange and removal abilities [49]. Overall, these results support the contention that elite rowers display anaerobic thresholds typically occurring at 85 to 95% VO_{2max} [31, 251, 267], reflecting a large capacity for aerobic energy supply at a high relative exercise intensity [12, 55].

During short duration (approximately 30 to 150 s) rowing exercise, the capacity to produce and maintain a high external power output is higher in successful compared to less successful rowers [28]. Riechman *et al*. [263] found peak (r = 0.85) and mean (r = 0.87) power output during an all-out effort 30 s rowing ergometer test to be among variables related to 2000 m ergometer performance. Pripstein *et al*. [36] reported maximum AOD, a measure of anaerobic capacity, to be significantly related to 2000 m rowing ergometer time trial performance. Over very brief periods of exertion (15 s or less), Ingham *et al*. [51] found that maximum power output (r = 0.95) and force production (r = 0.95) during a five-stroke rowing ergometer test were strongly correlated with 2000 m ergometer performance, results corroborated by Petrykowski & Lutoslawska [54] and Oglesby & Oglesby [56]. Interestingly, although knee extension and flexion peak isokinetic torque have been shown to be related to 2000 m rowing ergometer performance [35, 48, 56], maximum strength is not commonly considered associated with rowing performance among experienced rowers [254].

It is worth noting that most studies investigating rower characteristics related to superior performance have used rowing ergometer performance as the criterion measure. McNeely [262] reported that within a squad of international calibre heavyweight oarsmen no significant correlations were evident between 2000 m on-water rowing performance time and rowing ergometer-based measures of VO_{2max}, ventilatory threshold or anaerobic work capacity. The ability to produce and maintain an effective external power output is rewarded more easily during ergometer versus on-water rowing [35]. It is plausible that this may inflate the association between physical and physiological capacities and rowing performance somewhat [4] and is worth considering when interpreting the characteristics linked to superior rowing performance in the scientific literature.

Nonetheless, viewed in totality, the anthropometrical and physiological characteristics of successful rowers suggest a better capacity to produce and maintain a high power output and effectively transfer this into boat velocity [255]. While measures of endurance fitness like VO_{2max} and power output at submaximal transition thresholds are typically high in relative terms among endurance-trained athletes like cyclists and runners, successful rowers distinctively demonstrate very high values in absolute terms [264], largely a reflection of their larger body size and muscle mass in comparison to most endurance-trained athletes [10]. In rowing, a high selection pressure exists for stature, limb length and absolute indices of aerobic and anaerobic energy supply [4, 65, 253]. It is unknown whether performance is related to the proportional contribution to total energy supply by aerobic and/or anaerobic energy supply during rowing.

2.3.5 Rowing Ergometry

2.3.5.1 Background

Northern Europe and Scandinavia were among the most popular regions for competitive rowing in the late nineteenth and early twentieth centuries [34]. With training and racing during winter months severely restricted the desire for more rowing-specific preparation led to the design of rowing simulators and ergometers: land-based machines that simulate the rowing movement [13]. The development of the first rowing machine is credited to William Curtis in 1871 [34] while in 1925 Henderson & Haggard [11] appear to be among the first scientists to publish data on the physiological responses of rowers to simulated rowing exercise. Since the mid-twentieth century rowing ergometers have been used routinely in the training of rowers [34].

Among rowers and rowing coaches, besides representing the alternative training tool of choice away from on-water rowing [59], rowing ergometers are valuable tools for physical fitness assessment [4]. While races and the majority of training sessions are conducted on water [10], the controlled assessment of physiological parameters and performance indicators in rowers is complicated in this setting by the effect of weather and water conditions [268]. Assessing physical performance, acute physiological responses, and training adaptations in a rowing-specific modality has therefore largely been conducted using ergometer rowing [28]. The result is that rowing ergometers are now considered an essential tool for scientific research in rowing [269].

Ergometer-based assessment of rowers has taken the form of maximum effort performances over fixed durations of time [32] or more commonly nowadays, time trials over fixed simulated distances [47]. Incremental exercise formats remain popular for the laboratory assessment of rowers [51], permitting sport-specific exercise under controlled conditions for assessing VO_{2max}, submaximal transition thresholds or peak power output [4]. But the rowing ergometer assessment conducted most extensively by coaches and sport scientists remains a time trial over a simulated 2000 m distance on a Concept II rowing ergometer [14].

2.3.5.2 Concept II Rowing Ergometers

A variety of rowing ergometers have been developed [10]. The Concept II rowing ergometer is an air-braked variable resistance rowing ergometer with a freely moving seat on a central guide rail, or slide, a fixed foot stretcher and a centrally positioned flywheel, handle and chain, permitting a symmetrical rowing movement pattern more similar to on-water sculling than to sweep-oar rowing [13, 270]. Concept II rowing ergometers are the most commonly used land-based apparatus for training and assessment in contemporary rowing programmes [271] and have been updated through various models over several decades [269], but remain easy to maintain, portable and relatively inexpensive [270]. So popular is the Concept II rowing ergometer that it represents an additional rowing competition format internationally, with rowing ergometer indoor championships now held annually using this type of ergometer [271].

The Concept II rowing ergometer computer uses an algorithm to determine external power output based on flywheel moment of inertia, handle displacement and time, flywheel torque and chain gearing [269]. During every rowing stroke, the external power output calculated reflects the power output required to accelerate the flywheel and overcome air resistance [268], the latter being adjustable via a dampener on the ergometer which can increase or decrease the resistance, or drag [269]. Power output is recorded and displayed by the Concept II ergometer computer monitor using specific software rather than independently from handle force and displacement [268], along with other measured and derived parameters like time, stroke rate, simulated rowing distance completed or remaining, and average power output. The manufacturers claim the power output measurements to be accurate to within approximately 2% [272].

Importantly, differences between the air-braked Concept II rowing ergometer and the most popular predecessor, the mechanically-braked Gjessing ergometer appear to render physiological responses and performance specific to the ergometer type used [269]. Hahn *et al*. [270] reported significantly higher mean power output on a Concept II (256 W) compared to a Gjessing (234 W) rowing ergometer during a 7.0 min performance test in female rowers. Using an incremental exercise protocol, Lormes *et al*. [273] demonstrated significantly higher maximum power output and lower stroke rate during exercise on the Concept II versus Gjessing ergometer, with blood lactate responses yielding significantly higher anaerobic threshold values on the Concept II ergometer. The authors concluded that a different force-velocity relationship likely exists for the rowing stroke between the ergometer types, potentially influencing the extent and/or pattern of skeletal muscle involvement [273]. Despite excellent correlations (r = 0.97 to 0.99) between measures made on the two instruments [270, 273], the magnitude of difference in absolute and relative indices of power output, stroke rate and endurance fitness suggests that results of investigations of mechanical efficiency or energy expenditure during ergometer rowing should be considered particular to the ergometer type used [269].

2.3.5.3 Validity

In comparison to on-water rowing, ergometer rowing requires a simpler set of movements or technique, and it has therefore been suggested that laboratory measures obtained using ergometry may not be truly reflective of on-water rowing performance [266]. While correlations between performance on the two modalities are generally good [4], the best ergometer rowers are not necessarily the best on-water rowers, and *vice versa* [266]. It is difficult to infer on-water rowing performance, which incorporates additional movement skills, from rowing ergometer performance [35]. Balance, efficiency, coordination, blade (oar) work and other on-water rowing technical elements are neither required nor assessed during ergometer rowing [4]. Unsurprisingly, there are also differences in the energy demand between these rowing modalities [274]. As a result, the relevance to on-water rowing performance of ergometer-based measures like mechanical efficiency, VO_{2max}, submaximal transition thresholds and even time trial performance has been questioned [275].

Research results suggest similar VO_{2max} [276], mechanical efficiency [277] and anaerobic threshold [275] values when comparing on-water and ergometer rowing. At submaximal exercise intensities, HR, blood lactate and epinephrine responses between the modes have been shown to be statistically equivalent [278] while at maximum effort, the data is equivocal: some researchers have reported no significant differences in VO_2, HR, blood lactate concentration or rate of energy expenditure per unit time [59], while others have suggested significantly different lactate and HR responses [279] between 2000 m time trials conducted as on-water rowing and simulated ergometer races. Beyond physiological responses, Ryan-Tanner *et al*. [280] reported moderately strong correlations (r = 0.74) between on-water and Concept II rowing ergometer 2000 m time trial performance. More recently, significant relationships have been demonstrated between 2000 m rowing ergometer time trial performance and final ranking at rowing world championship events in most boat classes for elite junior [281] and senior [282] rowers. From this data it appears that, at the very least, similar physiological factors contribute to both on-water and ergometer 2000 m rowing performance [280].

Further, ergometers simulate many of the biomechanical demands of rowing [13]. Elliot *et al*. [283] reported that only one parameter (knee joint angle) was significantly different between ergometer and on-water rowing. Lamb *et al*. [284] found significant differences only in arm kinematics between ergometer and on-water rowing, likely the result of on-water oar manipulation, yet the authors still concluded that the ergometer appropriately simulated on-water rowing. Kinematic and electromyographic comparisons between on-water and ergometer rowing have revealed that the major leg and trunk movements, the primary force-producing actions in rowing [256], are very similar between the two modalities [285].

To summarize, rowing ergometers provide a close approximation of the rowing stroke and permit the accurate and standardized physiological assessment of rowers [13]. The specificity of on-water assessment of rowers is arguably greater but this remains impractical in all but the most ideal environmental circumstances, since weather and water conditions may hamper data collection procedures or influence rower power output and physiological responses [275]. While no studies have yet compared the kinematics and kinetics of on-water rowing and the Concept II rowing ergometer specifically, most studies support the use of ergometers to simulate the biomechanical demands of on-water rowing [13]. The similarity in physiological responses between the two modalities supports the use of ergometer rowing as a valid and representative simulation of the physical demands of on-water rowing and assessing rowing-specific physical performance [269].

2.3.5.4 Reliability

Evidence suggests that rowing ergometry allows reliable assessment and monitoring of rowing-specific physical performance [230, 271, 286-289]. Soper & Hume [271] assessed the reproducibility of a Concept II rowing ergometer time trial by measuring the standard error of measurement between repeated 2000 m performances and found it to be 1.3% for mean power output, concluding that its reliability made it an appropriate modality to use for rowing-specific physical performance assessment [271]. Schabort *et al*. [289] reported a high (r = 0.96) test-retest correlation and low coefficient of variation (2.0%) when investigating individual variability in mean power output during a 2000 m time trial on a Concept II rowing ergometer. Based on time to completion, the typical error associated with the 2000 m rowing ergometer time trial, expressed as percentage coefficient of variation is reportedly between 0.5% and 0.6% [230, 289]. Additionally, Henry *et al*. [287] reported a higher test-retest correlation for peak (r = 0.94) and average (r = 0.96) power output during 30 s of high intensity rowing on a Concept II ergometer than on other ergometer models tested. The high reliability of the Concept II rowing ergometer has been suggested as stemming from its relatively simple design and widespread familiarity among rowers [28], likely in conjunction with the ability of experienced rowers to reproduce remarkably comparable rowing stroke characteristics [288].

2.3.5.5 Summary

Concept II rowing ergometers provide valid and reliable simulations of on-water rowing and elicit similar physiological responses [271]. The advantage of being able to standardize assessment conditions would seem to outweigh the limitations of differences between ergometer and on-water rowing, at least when the main goal is monitoring physiological responses and capabilities relevant to rowing [12]. The majority of studies that have measured physiological and performance data on rowers have done so using ergometer-based assessment [269]. In practice, the simulated 2000 m time trial conducted on a Concept II air-braked rowing ergometer continues to be used internationally as the most fundamental representation of rowing-specific physical and physiological capacity [14].

2.3.6 Physiological Demands of Rowing

2.3.6.1 Background

As early as 1868, scientific interest in the physiological demand of rowing was already under way judging by Fraser's [252] report on the HR response of oarsmen before and after on-water rowing. While the nature and magnitude of acute physiological responses to rowing has been studied extensively since then [10], most investigations have involved heavyweight male rowers, making information on lightweight and female rowers scant by contrast [254]. Additionally, some rowing competitions are staged over distances as short as 200 m or as long as trans-oceanic crossings, but the standard international competitive distance is 2000 m [255]. It is data describing the physical and physiological demands of this event which will be presented in this section as background to the underlying internal metabolic cost of rowing discussed in the final sections of this review.

2.3.6.2 Neuromuscular Demands

Simply, rowing may be described as dynamic, whole-body exercise involving many skeletal muscle groups [251] but such a description belies its submission as the most physically demanding of endurance sports [12]. The standard 2000 m rowing distance has been termed a power-endurance event [28] since large forces must be generated during every stroke to propel the boat effectively, and a high power output must be maintained for the duration of the race, typically 5.5 to 7.5 min depending on competitive category and environmental conditions [10]. It has been estimated that rowing at competitive race pace involves static and dynamic force production by around 70% of a rower's muscle mass in producing rowing power output averaging 450 to 550 W for elite heavyweight men [264]. Force applied to the oar per stroke approximates 1000 to 1500 N during the start and settles at around 500 to 700 N during most of the remainder of a rowing race [266]. Depending on competitive category and boat class a 2000 m race may require 210 to 250 sequential rowing strokes to complete, usually at a stroke rate averaging 32 to 38 strokes·min^{-1} [255]. In comparison to running and cycling, rowing imposes duty cycles which are heavier and slower, implying higher forces and lower shortening velocities by a larger proportion of skeletal muscle mass [255]. In addition, essential technical elements of competitive rowing, including balance, force-time characteristics of body movements during the rowing stroke, and synchrony with crew members impose additional neuromuscular demands during rowing [266].

2.3.6.3 Regulation of Effort (Pacing)

While the neuromuscular demands of rowing are unique, the profile of power output most commonly adopted for a 2000 m rowing race is characteristic of other sporting events of similar performance duration, like middle-distance running [130, 290]. Power output is very high for about 40 s after the start and demands large muscular forces and a high stroke rate—around 40 to 50 strokes·min^{-1} [12]. The first 500 m is often the fastest quarter of a rowing race, speculated as providing a tactical and psychological competitive advantage as well as augmenting the stimulation of aerobic energy supply in active muscle [94, 130, 290] albeit at a higher energy cost to the rower [254]. The middle section of a race is characterized by a reduced stroke rate of around 32 to 38 strokes·min^{-1} for 4.0 to 4.5 min before being increased during attempts to raise power output toward the finish [12]. Interestingly, simulated rowing races on ergometers show comparable pacing profiles [290], suggesting that neurobiological feedforward and feedback mechanisms regulating effort are similarly involved in competitive on-water and simulated ergometer rowing races [130].

2.3.6.4 Cardiovascular Responses

Heart rate routinely reaches 180 to 200 $b \cdot min^{-1}$ during maximum effort rowing [12]. Rowing elicits lower HR responses compared with running at comparable relative submaximal exercise intensities and at maximum effort [291]. This is likely a result of higher venous return and augmented central blood volume in rowing as opposed to running secondary to the seated body position and peripheral venous pump action by a larger active skeletal muscle mass [10]. Heart rate tends to be lower during on-water compared to ergometer rowing [12]. As in other forms of exercise, HR and VO_2 are linearly related during incremental exercise for both ergometer and on-water rowing through a range of submaximal intensities [253].

2.3.6.5 Ventilatory Responses

High intensity rowing routinely elicits pulmonary ventilation rates of 165 to 200 $L \cdot min^{-1}$ in elite rowers depending on competitive category [96, 277] with mean values over 200 $L \cdot min^{-1}$ being regularly reported during on-water rowing races in heavyweight men [12]. Breathing becomes entrained during rowing, meaning that ventilatory cycles are performed in a temporal rhythm related to body movement and stroke rate [292]. The high work demand placed on respiratory muscles during rowing contributes considerably to the energy expenditure of rowing [293]. While it has been suggested that the cramped body position maintained through the catch phase of the rowing stroke and the seated body position in rowing may impair ventilation, preventing it from reaching a mechanical optimum [294], evidence suggests that gas exchange is not compromised during rowing, with the respiratory equivalent during rowing comparable with other endurance activities [12], and maximum minute ventilation achieved during rowing typically higher than during running [52].

2.3.6.6 Neuroendocrine Responses

Plasma catecholamine concentrations following maximum effort rowing have been found to be around twice that noted after running [251], highlighting the magnitude of systemic physiological stress imposed by rowing. Epinephrine and norepinephrine concentrations 20- to 30-fold resting values have been measured following maximum effort ergometer rowing [149]. Plasma adrenocorticotrophic hormone and cortisol are markedly elevated following rowing [295]. Testosterone and growth hormone concentrations are increased following supramaximal but not submaximal intensity rowing, as are insulin-like growth factor 1 (IGF-1) and glucose, while insulin concentration is decreased [296]. While the directions of these responses are typical of acute exercise, their magnitude underscores the extent of hypothalamic-pituitary-adrenal and sympathoadrenal stimulation elicited in supporting the physiological demands of high intensity rowing [4].

2.3.6.7 Summary

Measurements made during competitive on-water or simulated ergometer rowing races attest to the severity of the physiological demand which the 2000 m event imposes [255]. The combination of high force application per stroke, extensive skeletal muscle involvement, and repetition of a unique movement pattern distinguish the demands associated with competitive rowing from other locomotive sport activities like running and cycling [10]. These demands are associated with profound acute systemic physiological adjustments—many of them involved in altering skeletal muscle O_2 and substrate availability—suggesting that whole-body energy expenditure during rowing is high [4, 12]. The remaining section of this review details the nature and magnitude of this energy expenditure before examining previous studies attempting to elucidate the relative contribution of aerobic and anaerobic energy supply in meeting this demand.

2.3.7 Energy Expenditure during Rowing

2.3.7.1 Rowing Efficiency

Mechanical efficiency describes the relationship between total internal metabolic energy expenditure and effective external mechanical work performed [253]. The external mechanical energy cost of on-water rowing reflects mainly the drag resistance to the boat moving in the water and the air resistance to the motion of the boat, oars and rower(s) [10]. On contemporary air-braked rowing ergometers like the Concept II apparatus, external mechanical energy cost reflects the air resistance to flywheel motion and frictional forces of the chain system [65]. The internal metabolic cost for a rower during on-water rowing is a sum of two components: 1. the energy expended to propel the boat by delivering force onto the oars and footboard, dependent on how hard the rower pushes and pulls; and 2. the energy expended in moving the body in the boat against friction and gravity, dependent on the rower’s body mass and stroke rate [10, 294]. On a rowing ergometer these are replaced by, respectively, the energy expended in exerting force on the handle and footboard to accelerate the flywheel, and in moving the body to and fro on the ergometer sliding seat [32].

Attempts have been made to quantify that part of the internal metabolic cost during rowing associated with simply moving the body as opposed to producing the rowing power output. Studies of unloaded rowing report mean VO_2 values at 20 and 36 strokes·min^{-1} of around 1.2 and 2.9 L·min^{-1} respectively, and besides stroke rate, are likely dependent on the body size of the rowers studied [32, 254]. During on-water rowing, this fraction of the internal metabolic cost is not fruitless since body movement during the recovery phase of the stroke in highly skilled rowers assists the forward motion of the boat, meaning that a large fraction of the O_2 cost of unloaded rowing may have a contributing role in boat acceleration and therefore performance [294]. No such benefit exists during ergometer rowing, in which only energy expenditure contributing to accelerating the fan against air resistance is recorded as effective external power output [28]. This is only possible during the drive phase, while the recovery phase on an ergometer only contributes to the internal metabolic cost to the rower [65]. Further, the work of moving the body on the seat is greater in ergometer rowing than in on-water rowing [266]. In rowing, the boat is pushed through the water by the force transmitted onto the footboard and oars and ultimately to the water, with the body remaining relatively still in space during the subsequent recovery phase, since the moving boat is essentially received under the rower [255]. In ergometer rowing, the body must be displaced up and down the slide for each stroke, and only force directed into the drive phase of the stroke contributes to external power output [274]. Further, as stroke rate increases, the additional energy cost of moving the body back and forth is greater in simulated versus on-water rowing, resulting in ergometer rowing eliciting a higher internal energy expenditure for a given external power output and possibly accounting for the lower mechanical efficiency of ergometer versus on-water rowing [253].

The efficiency of on-water and ergometer rowing is influenced by rowing intensity and stroke rate [32]. Di Prampero *et al*. [253] reported that rowing mechanical efficiency was 18% at 25 strokes·min^{-1} and increased with stroke rate to 23% at 37 strokes·min^{-1}. Similarly, Secher [254] reported the mechanical efficiency of rowing at racing speeds as approximating 22%. As far as ergometer rowing is concerned, as early as 1925 Henderson and Haggard [11] measured rowing efficiencies between 20% and 25% during exhaustive simulated rowing efforts. Subsequent reports on mechanical efficiency during simulated rowing have corroborated those early findings, with mean values around 20% reported for ergometer rowing and a range of approximately 16% to 24% [12]. Droghetti *et al*. [32] described net mechanical efficiencies averaging 19% at submaximal intensity and 21% at race pace on a rowing ergometer. More recently, studies utilizing Concept II rowing ergometers have yielded gross efficiencies of 19% during submaximal stages of an incremental exercise test [53] and net efficiencies of 20 to 21% during simulated 2000 m time trials [35, 59].

2.3.7.2 Total Energy Demand

Rowing at a competitive boat velocity or a power output characteristic of an ergometer time trial is associated with a high rate of energy expenditure [253]. In support of this contention is the consistent observation of high VO_2 values during both on-water and ergometer rowing, since VO_2 reflects the rate of aerobic energy supply [12]. Jackson & Secher [297] measured VO_2 values between 6.0 and 6.5 $L \cdot min^{-1}$ during high intensity on-water rowing in the single, double and pair boats in two champion heavyweight oarsmen, while Hagerman *et al*. [30] frequently measured values above 6.0 $L \cdot min^{-1}$ during a 6.0 min maximum effort rowing ergometer test in 310 international male rowers. These high absolute values are partly a product of the large body size of the heavyweight male participants in these observations [10], but they do attest to the high energy expenditure associated with performing the rowing action. Indeed, rowers and untrained individuals have been shown to achieve VO_{2max} values 4% to 5% higher during ergometer rowing compared to treadmill running [52, 138], likely a result of more intensive involvement of a larger skeletal muscle mass [254]. Unsurprisingly then, rowing has been described as one of the most energetically demanding exercise modalities [277].

Based on results from studies of rowing mechanical efficiency, the total energy cost of a race can be estimated from on-water rowing performance time or rowing ergometer mean power output [32]. The estimated energy expenditure, expressed as an equivalent VO_2, for rowing performances typical of elite competition or ergometer time trials over 2000 m approximate 7.0 $L \cdot min^{-1}$ in heavyweight men, 6.0 $L \cdot min^{-1}$ in lightweight men, 5.5 $L \cdot min^{-1}$ in heavyweight women and 5.0 $L \cdot min^{-1}$ in lightweight women [12, 41, 254, 294]. Energy expenditure is typically higher for more compared to less accomplished rowers—internationally competitive heavyweight men displayed energy expenditure of 37 $kcal \cdot min^{-1}$ over a simulated rowing race lasting 6.0 min [12] in contrast to 24 $kcal \cdot min^{-1}$ by less accomplished rowers in ergometer races lasting closer to 7.0 min [59]. Unsurprisingly then, the estimated total energy cost of rowing at internationally competitive boat velocities is estimated to have increased by around 1.3 $L \cdot min^{-1}$ over an eighty year period, congruent with the improvement in competitive rowing performance [254].

2.3.7.3 Summary

The net mechanical efficiency of rowing is in the range of 18% to 22% [264] with differences between ergometer and on-water rowing as a result of distinct mechanical, propulsion and technical characteristics of the modalities [32, 253, 254]. Energy expenditure during rowing at race pace is very high and is influenced by rower body size and physical capacity [12], stroke rate [32] and mechanical efficiency [253]. Differences in reported values for energy expenditure, efficiency and metabolic cost of ergometer rowing are thus likely a result of differences in rower calibre and competitive category, stroke rate, rowing performance time and ergometer type between investigations.

2.3.8 Aerobic and Anaerobic Energy Supply during Rowing

Based on VO_2, HR and power output, Hagerman *et al*. [277] described the physiological demand of maximum effort 2000 m on-water and ergometer rowing as severe. In simulated races, the majority of time after the first minute is spent at near maximum (around 95-98% VO_{2max}) rates of aerobic energy supply [12, 36, 37, 298], and peak VO_2 during a race simulation has been shown to match VO_{2max} measured during a progressive incremental exercise test [36, 96, 230]. Whole-body VO_2 may be elevated 15- to 20-fold resting values, commonly exceeding 6.0, 5.0 and 4.0 $L \cdot min^{-1}$ during rowing ergometer time trials in heavyweight men, lightweight men and women, respectively [277]. Yet, as recognized nearly a century ago by Henderson & Haggard [11], the highest attainable VO_2 is still insufficient to fully support the energy cost associated with mean boat velocity or power output achieved during on-water or simulated rowing races. Secher [254] alleged a deficit in O_2 utilization equivalent to 0.3 to 0.5 $L \cdot min^{-1}$ when rowing at race pace. Despite high rates of aerobic ATP supply, anaerobic energy provision must therefore contribute significantly to the energy demand of 2000 m rowing races or simulations [32].

Evidence of elevated skeletal muscle anaerobic energy supply during rowing is provided by the high blood lactate concentration typically measured after on-water or ergometer rowing races [30]. Post-race peak blood lactate concentration is commonly in the range of 11 to 19 $mmol \cdot L^{-1}$ [12] and possibly as high as 26 $mmol \cdot L^{-1}$ [10]. The degree to which anaerobic energy capacity is taxed during competitive rowing was highlighted when Pripstein *et al*. [36] demonstrated that total anaerobic energy yield, as measured by AOD, was as large during a 2000 m time trial as during a 2.0 min all-out effort exercise bout designed to exhaust anaerobic capacity. Anaerobic

ATP supply mechanisms appear to be used throughout a rowing race but to a greater degree during the initial 60 to 90 s when very high power output is required during the start phase to overcome the inertia of the boat and attain racing velocity [130]. Since it takes around 60 to 90 s for VO_2 to reach near-maximum rates during a rowing race [36, 96], a substantial portion of the energy demand during this initial period is met by anaerobic metabolism [37]. Acceleration towards the end of a rowing race is likely also supported mostly by augmented anaerobic ATP supply, since during this stage only modest increases in VO_2 have been observed and VO_2 is already at, or very near maximum by that time [36, 96, 230].

While quantifying aerobic energy supply during rowing based on VO_2 has long been considered routine [12], assessing the anaerobic energy system contribution has remained problematic. As in studies using other exercise modalities, several measures have been used to estimate anaerobic energy supply during rowing, including the O_2 debt [30, 59], O_2 deficit [29, 32, 35-37], and post-exercise blood lactate concentration [59]. To highlight the evolution of methods and different results over time, the results of these investigations will be considered chronologically.

Parallel with early efforts to characterize the relative contribution of energy supply systems to exercise bouts of different durations [88, 89] Szogy & Cherebetiu [218] reported proportional aerobic (68%) and anaerobic (32%) energy supply during 6.0 min of strenuous exercise in thirty-two competitive oarsmen using the AOD method, but employed ergometer cycling as the exercise modality. Therefore Hagerman *et al*. [29] appear to have published the earliest report on relative energy system contributions during rowing-specific exercise. These researchers studied the metabolic responses of twelve internationally competitive female rowers during 4.0 min of simulated rowing. Accumulated O_2 uptake was obtained using VO_2 measured every minute and integrated over the duration of the exercise bout, and was used to calculate aerobic energy supply. A mean O_2 deficit of 4.4 L was measured and was used in conjunction with an assumed energy expenditure equivalent of O_2 to calculate relative aerobic and anaerobic energy system contributions respectively of 70% and 30% of the estimated total energy demand of the rowing task [29].

Subsequently, investigators from the same research group [30] measured VO_2 during 6.0 min of exhaustive rowing ergometer exercise and during 30.0 min of active recovery thereafter in international male rowers over a ten year period. Net accumulated O_2 uptake measured during exercise was used to calculate aerobic energy supply, while O_2 debt was used to represent anaerobic energy supply during the preceding maximum effort rowing task. Assuming an energy expenditure equivalent for O_2 of 5 kcal·L^{-1} these researchers, albeit with an alternative method, corroborated the results of their earlier work in establishing relative aerobic and anaerobic energy supply contributions during the simulated rowing performance to be 70% and 30%, respectively [30].

Mickelson & Hagerman [31], while using respiratory gas exchange measures to study endurance fitness in members of a national rowing squad, commented on the energy system contributions to rowing exercise in an as yet unrepeated manner. Twenty-five male rowers performed incremental exercise on a mechanically-braked rowing ergometer to determine VO_{2max} and anaerobic threshold. The authors reported that rowers could generate around 72% of their power aerobically since this represented the mean percentage of maximum power output at which anaerobic threshold occurred during the incremental rowing test [31]. While subsequent reports [4, 35] have included these results in discussing energy system contributions during rowing, it seems unlikely that the interpretation and methods of Mickelson & Hagerman [31] can be generalized to represent aerobic and anaerobic energy supply during a maximum effort 2000 m rowing ergometer time trial performance.

A 1982 report by Secher *et al*. [299] described how accumulated O_2 uptake was calculated as an indication of total aerobic energy supply during 6.0 and 4.0 min of all-out effort rowing ergometer exercise in international calibre male and female rowers respectively. While post-exercise VO_2 measures were also reported in the study as an indication of anaerobic energy supply during the preceding exercise, curiously, these particular recovery measurements appear to have been made following exercise on a modified cycle ergometer rather than after the rowing ergometer VO_2 measures. Relative aerobic and anaerobic energy supply was not calculated for the rowing ergometer exercise by these researchers [299] but appears to have been done retrospectively and reported by others [4, 35], with a range of 70% to 86% for relative aerobic energy supply purported, although the procedures used for the subsequent analysis are not apparent.

Droghetti *et al.* [32] investigated the energy expenditure associated with a maximum effort 6.0 min rowing race simulation on a mechanically-braked ergometer in nineteen members of a national rowing team. Total energy cost was determined from a VO_2-PO relationship established using VO_2 measured during three 3.0 min ergometer exercise bouts at intensities approximating

200, 250 and 300 W, plus the estimated O_2 cost of race-specific stroke rate determined from measurements made during unloaded rowing. The O_2 deficit was measured to determine anaerobic energy supply using the difference between mean VO_2 measured during the ergometer race and the estimated total energy demand of the race, expressed as a VO_2 equivalent. The investigators reported aerobic and anaerobic energy system contributions of 80% and 20% respectively [32].

Russell *et al*. [35] calculated the anaerobic energy system contribution during a 2000 m time trial performance on a Concept II air-braked rowing ergometer to be around 16% in a group of elite schoolboy rowers. In establishing a VO_2-PO regression model, these investigators made use of three discontinuous submaximal intensity exercise bouts of 5.0 to 7.0 min in duration, approximating 70%, 80% and 90% of mean power output achieved in the 2000 m time trial, combined with a fixed y-intercept of 5.0 $ml \cdot kg^{-1} \cdot min^{-1}$. The AOD was measured as the difference between estimated VO_2 demand and mean VO_2 during exercise, with the latter accounting for the remaining 84% aerobic contribution to total energy demand [35].

Pripstein *et al*. [36] appear to have been the first investigators to publish information on relative energy system contributions in female rowers during a 2000 m rowing ergometer race simulation. Four 4.0 min submaximal intensity stages of an incremental exercise test approximating 35%, 50%, 70% and 85% VO_{2max} were used to establish a linear VO_2-PO relationship. Using the accumulated O_2 uptake and deficit over the duration of the 2000 m rowing ergometer performance these researchers estimated that well-trained female club rowers derived 88% and 12% of the total energy requirement of the time trial from aerobic and anaerobic supply mechanisms respectively [36].

Martin & Roberts [37] presented similar results on the energy system contributions during a maximum effort 2000 m rowing ergometer time trial in four national level heavyweight oarswomen. In addition to reporting relative aerobic and anaerobic energy system contributions of 89% and 11% respectively, these investigators showed that almost two thirds of the anaerobic energy supply contribution was made within the first two minutes of the rowing race simulation [37].

More recently, de Campos Mello *et al*. [59] calculated and compared the relative energy system contributions during 2000 m rowing races performed during two different ergometer conditions and actual on-water rowing in eight non-elite male rowers. It appears that this is the only study to date to measure proportional aerobic and anaerobic energy supply during an on-water rowing race. These researchers established the aerobic energy supply contribution from net VO_2 over the duration of the rowing performances. Anaerobic energy system contribution was estimated from a combination of EPOC and a VO_2 equivalent for post-exercise blood lactate concentration. Using an energy expenditure equivalent for O_2 of 5 $kcal \cdot L^{-1}$ to establish total energy expenditure, aerobic and anaerobic energy supply was reported to represent 84% and 16% of this total, respectively [59].

Clearly, initial investigations into the energy system contributions during rowing made use of exercise formats and/or an ergometer type which are no longer popular—a fixed duration 4.0 or 6.0 min rowing race simulation on a mechanically-braked ergometer—in arriving at relative aerobic energy supply contributions of between 70% and 80% of total energy demand [29-32]. While these results remain commonly cited in rowing coaching literature [33, 34] the relevance of these studies to contemporary performance tests may be questioned on two fronts. Firstly, studies have shown that air-braked and mechanically-braked rowing ergometers elicit different power outputs, stroke rates and physiological responses [270, 273]. Secondly, differences in performance duration and pacing pattern between fixed duration and fixed distance exercise formats may be reasonably hypothesized, with the latter better simulating the requirements of competitive rowing [10, 12, 255]. Both these factors have the potential to influence aerobic and anaerobic energy supply during maximum effort rowing exercise [110, 115, 255]. If the results of initial studies are excluded on these bases, event-specific data on the relative contributions of energy supply systems during on-water or ergometer rowing performances is lacking. Only a few investigations [35-37] have employed the preferred AOD measurement technique in combination with a 2000 m rowing ergometer time trial on a Concept II rowing ergometer, despite this method being recommended for the assessment of anaerobic energy supply in rowers [28]. Of these studies, only one [35] accounted for resting VO_2 by expressing net rather than gross energy system contributions during the rowing performance and none appear to have accounted for peripheral O_2 stores in reporting aerobic and anaerobic energy yield, as is popularly recommended when using the AOD method [216]. The effect of calculating relative energy supply contributions with or without consideration of these factors does not appear to have been investigated. So while aerobic energy supply likely predominates during competitive rowing performances [60], in light of methodological shortcomings in earlier studies, discrepancies in data reporting, and the scarcity of current, event-specific information, a need exists to clarify the extent of this dominance.

2.3.9 Summary and Research Problem

Competitive rowing requires the maintenance of a high power output for several minutes through the involvement of a major proportion of skeletal muscle mass in a motor pattern and body position unique among cyclic exercise modalities [255]. Rowing at race pace demands several physiological capacities and responses be taxed to near maximum levels [4]. Time to complete a fixed 2000 m distance represents the performance criterion in rowing, with the morphology and physiology of successful rowers reflecting the ability to produce effective force and sustain a high power output [10]. The nature of the sport, characteristics of elite participants and typical physiological responses elicited suggest that rowing imposes large demands on the rate and capacity of both aerobic and anaerobic energy supply [12]. Owing to its validity in simulating the physical demands of on-water rowing and its reliability, practical utility and familiarity within the rowing community, the Concept II air-braked rowing ergometer has become the most popular land-based tool used in the training and assessment of competitive rowers [269]. A maximum effort fixed distance 2000 m time trial on this ergometer has become the standard physical performance test for rowers [4].

Despite limitations in the methodology of early studies, results of previous investigations into the energy system contributions during rowing collectively suggest that relative aerobic energy supply during a 2000 m on-water and/or ergometer rowing performance may be appreciably higher than some published models on the theme propose. For example, some traditional exercise physiology texts purport a relative contribution from aerobic energy supply approximating only 50% to 60% of total energy demand during competitive rowing and events with similar performance times [16, 19]. These models appear to be based largely on the results of original investigations into energy system involvement during exercise which used techniques which have since been discredited and which employed only cycling and running modalities [38-40]. Anaerobic energy supply, as measured by AOD, is significantly related to indices of body size [133], is higher during ergometer rowing than treadmill running [141], and is highly task- and event-specific [124, 142, 144]. In terms of athlete morphology, successful rowers are typically taller and heavier than other endurance sport competitors [10], while in terms of exercise modality, rowing involves a larger proportion of skeletal muscle mass and a fundamentally different body position compared to other locomotive or ergometer exercise activities [255]. Therefore, it seems reasonable to query estimations of relative energy system contributions in rowing based on studies employing other exercise modalities and/or athletes [26]. A need exists to challenge or corroborate traditionally and popularly reported energy system contributions during rowing with empirical data obtained during an event-specific exercise task using an updated and accepted method.

Models of relative aerobic and anaerobic energy supply during maximum effort exercise tasks suggest a higher proportion of anaerobic attributable energy supply in events with shorter performance times [16-19, 60]. This lends support to the hypothesis that faster rowing performance times may be associated with a higher anaerobic energy system contribution [35]. Indeed Secher *et al*. [41] hypothesized that the performance advantage of larger rowers may be derived from a larger anaerobic capacity owing to a larger muscle mass. Many studies have confirmed a relationship between rowing performance and measures of body size [35, 41, 43-45], the capacity for aerobic energy supply [35, 36, 41, 43, 47, 50-53, 56] and short duration force production and power output [35, 48, 51, 54, 56], but only Pripstein *et al*. [36] have reported maximum AOD, an indication of the capacity for anaerobic energy supply, to be significantly related to rowing ergometer time trial performance. While competitive rowing clearly demands a high capacity for both aerobic and anaerobic energy supply, whether rowing performance is related to the relative contribution of aerobic and/or anaerobic energy system supply during a maximum effort time trial does not appear to have been investigated.

The main aims of this study were therefore to: 1. quantify the relative contributions from aerobic and anaerobic energy supply during a 2000 m time trial on a Concept II rowing ergometer in national and international calibre oarsmen using the AOD method, with consideration of resting VO_2 and peripheral O_2 stores; and 2. determine the strength of the correlations between performance time and measures of both aerobic and anaerobic energy supply during the rowing ergometer time trial.

CHAPTER 3

MATERIALS & METHODS

3.1 Background

The research design, participant recruitment, measurement instruments, procedures and data analysis employed in this study are described in this chapter. Appendices referred to in this chapter are included as supplementary items at the end of this dissertation. A research proposal detailing the procedures and congruent with the World Medical Association's Declaration of Helsinki regarding ethical experimentation and good clinical practice in research involving human subjects was presented to the University of Pretoria's Faculty of Health Sciences Research Ethics Committee, and found to be acceptable without any recommended amendments (protocol number: S134/2007). A copy of a letter to this effect is provided in Appendix A.

3.2 Research Design

A quantitative, cross-sectional research design was employed such that empirical data was collected from a sample section of the rowing population during a single observation period in order to describe the phenomena investigated at a particular point in time [61]. Specifically, a descriptive and correlational study was designed to quantify the relative contributions of the aerobic and anaerobic energy supply systems during the performance of a 2000 m rowing ergometer time trial, and to assess the strength of the correlations between measures of energy system involvement and rowing ergometer performance.

3.3 Participants

A convenience sample of twenty-five (N = 25) healthy, well-trained male rowers aged 18 to 32 years volunteered to participate in the study. All were active members of the Rowing South Africa high-performance programme in the senior or under-23 competitive rowing categories at the time of the study, and all were nationally or internationally competitive rowers in their respective boat classes. The sampling method yielded volunteers who were experienced rowers exposed to similar training loads before and during the study period, and who were familiar with both laboratory exercise test procedures and ergometer rowing as a result of their systematic involvement in scientific assessment and regular ergometer training. At the time of the study the participants were engaged in routine rowing training with approximately 12 to 14 training sessions per week, of which at least six involved on-water or ergometer rowing. The sample included both scullers (n = 5) and sweep oar rowers (n = 20) from both heavyweight (n = 9) and lightweight (n = 16) competitive categories, but lightweight rowers were not required to attain official competitive body mass during this study. The study was limited to male participants only since the number of available female rowers at the same representative competitive level was limited at the time of the study.

Table 3.1: Participant inclusion, exclusion and discontinuation criteria.

Inclusion criteria
• Male. • Active involvement in training within the national rowing squad. • National and/or international competitive rowing representation within the twelve months prior to the study.
Exclusion criteria
• Known cardiovascular, respiratory or metabolic disease. • Acute illness or medication use, either at the time of the study or within the prior six weeks. • Adherence to any specialized dietary and/or nutritional supplementation intervention programme, either at the time of the study or within the prior six weeks. • Injury precluding participation in or likely to be aggravated by, the procedures involved in the study.
Discontinuation criteria
• Failure to adhere to test procedures or participant instructions. • Sustaining injury during exercise testing or during the study period precluding, or likely to be aggravated by, the procedures involved in the study. • Developing acute illness (e.g. upper respiratory tract infection) during the course of the study. • Performing physical training other than the standardized national rowing squad training programme during the course of the study. • Changes in habitual dietary practices during the course of the study.

An orientation session was conducted during which the study purpose, procedures, risks and potential benefits were explained, after which volunteers provided written informed consent to participate (Appendix B). This was followed by: written completion of a questionnaire to obtain information on participant demographics, recent and long-term health, training and rowing experience (Appendix C); provision and discussion of participant instructions pertaining to the study period (Appendix D); and an opportunity to have questions regarding the study answered by the investigator. Factors constituting cause for discontinued participation in the study were also explained. Based on their responses in the questionnaires the participants were screened according to the inclusion and exclusion criteria listed in **Table 3.1**. All twenty-five volunteers met the inclusion criteria and adhered to the required procedures during the study, and therefore none were excluded as participants.

3.4 Procedures

3.4.1 General Procedures and Participant Preparation

All measurements were made in the exercise testing laboratory of the Institute for Sport Research at the High Performance Centre, University of Pretoria—a facility conforming to general recommendations for exercise testing facilities [300]. This facility is situated at an altitude of approximately 1340 m above sea-level, and barometric pressure remained between 655 and 660 mmHg for the duration of the study. Laboratory temperature (18-20°C) and relative humidity (RH, approximately 50%) were continually monitored and controlled during all measurements. All procedures were performed by one investigator appropriately accredited and experienced in the measurement methods and data analysis procedures.

All measurements were conducted within a 14-day period during the South African domestic competitive rowing season. For each participant measurements were recorded during two separate visits to the exercise testing laboratory spanning a period of five days: the first visit included anthropometric assessment followed by a 2000 m rowing ergometer time trial, while the second visit included an incremental exercise test on a rowing ergometer. To control for diurnal variation in exercise performance and/or physiological response to exercise, each participant’s tests were conducted at the same time of day on each occasion. Participant compliance with instructions for the study period was assessed before every test; full details of these instructions are included in Appendix D. In particular, participants were required to be in good health during the study and well rested on the days of exercise testing. While participants continued with routine training throughout the course of the study, the training programme involved no unaccustomed exercise, no resistance training, and no changes in the training intervention within this period. Participants did not train on the day of an exercise test, and the day before a test included only a standardized and familiar low intensity endurance training session. Participant instructions regarding nutritional intake during the study were designed in attempt to standardize the timing and nature of pre-test food and fluid consumption and to avoid low muscle glycogen stores. Athletes were instructed to avoid alcohol and ergogenic aids (e.g. caffeine, sodium bicarbonate) for the 24 hours prior to an exercise test. Participants were asked to refrain from food intake within the three hours prior to a test although water intake was permitted *ad libitum* in the lead-up period to each test.

3.4.2 Specific Test Procedures

3.4.2.1 Anthropometry

In a suitably private area of the setting each participant underwent anthropometric assessment according to the participant preparation and measurement methods described by Norton *et al*. [301]. All measurements were made in accordance with those advocated by the International Society for the Advancement of Kinanthropometry (ISAK) [302] and were recorded on a data sheet (Appendix E) for subsequent analysis. Body mass was measured to the nearest 0.1 kg using a Tanita BF-350 electronic scale (Tanita Corporation, Tokyo, Japan) while stature was recorded to the nearest 0.1 cm using a Seca 214 stadiometer (Seca Corporation, Hanover, USA). Subcutaneous skinfold thickness at the triceps, subscapular, biceps, supraspinale, abdominal, mid-thigh, and medial calf skinfold sites [302] was measured to the nearest 0.1 mm using a Harpenden skinfold caliper (British Indicators Ltd., UK). These were summed to obtain the sum-of-seven skinfolds [301].

3.4.2.2 2000 m Rowing Ergometer Time Trial

Each participant performed a 2000 m time trial on a Concept II, Model D (Concept II, Morrisville, USA) rowing ergometer. This is the same rowing ergometer type and model that these rowers routinely used during laboratory exercise testing and indoor rowing training. The same individual ergometer was used for all tests by all participants to control for mechanical differences between ergometers influencing stroke resistance, rower workload or ergometer power output measurements. Prior to all tests the ergometer chain, seat, slide and computer were checked for cleanliness and normal operation according to manufacturer instructions. To prevent external movement of the ergometer it was secured with external weights on a non-slip surface further than 1 m away from any barrier in order to limit interference with the ergometer’s air braking mechanism [28]. The damper lever setting of the ergometer was adjusted to produce a standardized drag factor of 110 and 115 for lightweight and heavyweight participants respectively, the standard rowing ergometer drag factors routinely used by male rowers within the training squad of the participants and similar to values recommended [14].

A standardized 30.0 min warm-up protocol was implemented before the 2000 m rowing ergometer time trial which simulated the nature of the warm-up typically used by the participants prior to routine ergometer time trials. Participants performed 15.0 min of self-paced low intensity rowing on the same ergometer to be used for the time trial, followed by 10.0 min of alternating lower and higher intensity rowing. This consisted of 5 x 60 s rowing spells at a self-selected, progressively increasing intensity approximating the expected power output during the 2000 m time trial, interspersed with 60 s of low intensity rowing. A 5.0 min period of self-selected stretching activities followed. Finally, equipment for respiratory gas collection and heart rate (HR) monitoring was secured to the participant and its normal operation checked in preparation for the start of the time trial. A verbal start command for the time trial was given 5.0 min after the end of the warm-up.

Ergometer time trials were a standard feature of the scientific assessment and monitoring routine of the participants, ensuring all were familiar with the requirements for producing a maximum effort performance in this test. Participants were instructed to complete the 2000 m time trial in the shortest possible time, and strong verbal encouragement was provided throughout the test. Participants rowed in full view of the rowing ergometer computer which permitted visualization of elapsed time, simulated distance, stroke rate, power output and rowing pace expressed as time per 500 m. Participants were free to row at a self-selected stroke rate and according to an individually preferred pacing strategy during the time trial. Performance time (s), average power output (W) and average stroke rate (strokes$\cdot$min^{-1}) for the 2000 m time trial was obtained from the rowing ergometer computer after each test and recorded on a data sheet (Appendix E) for subsequent analysis.

During the time trial participants breathed through a Hans Rudolph 7400 series Vmask^{TM} low resistance facemask (Hans Rudolph, Inc., Shawnee, USA) which was firmly fitted before the start of the time trial and checked to ensure an air-tight seal. Pulmonary oxygen (O_2) uptake (VO_2) and carbon dioxide (CO_2) elimination (VCO_2) were calculated and recorded online for the duration of the test from open-circuit spirometry measurement of pulmonary ventilation and the fractional concentrations of expired O_2 and CO_2 respectively, using the Schiller CS-200 Ergo-Spirometer (Schiller AG, Baar, Switzerland). This fully automated metabolic cart determined the O_2 and CO_2 concentrations in expired air by means of paramagnetic and infrared methods respectively using a Power Cube (Ganshorn Medizin Electronic GmbH, Niederlauer, Germany) gas analyser. Pulmonary ventilation was measured with a Blendenspiroeptor (Ganshorn Medizin Electronic GmbH, Niederlauer, Germany) Silverman-type pneumotachometer, with expired ventilation adjusted to standard temperature, pressure and dry (STPD) conditions in calculating VO_2, as per convention [303]. Standard apparatus warm-up and calibration procedures for laboratory ambient temperature and barometric pressure, gas volume and gas concentrations were conducted prior to every test according to manufacturer instructions. In particular, a reference air sample with O_2 and CO_2 concentrations of 16% and 5% respectively was used for the gas analyser calibration and a 2.0 L syringe was used for the pneumotachometer calibration. While VO_2, expressed in both absolute terms ($L{\cdot}min^{-1}$) and relative to body mass ($ml{\cdot}kg^{-1}{\cdot}min^{-1}$) was measured continuously during the test, data was averaged and recorded for every 10 s time period. The Schiller CS-200 Ergo-Spirometer permitted continuous HR ($b{\cdot}min^{-1}$) measurement using electrocardiography, and values were averaged every 10 s and recorded. Individual participant cardiorespiratory data files were marked at the start and end of the rowing ergometer time trial, exported to spreadsheet format, and electronically stored for subsequent analysis. Peak VO_2 (VO_{2peak}) and peak HR (HR_{peak}) were recorded as the highest values obtained over any 30 s period (three consecutive 10 s recordings) during the 2000 m rowing ergometer time trial. Following completion of the 2000 m time trial participants were disconnected from the respiratory gas collection equipment and performed 5.0 to 10.0 min of low intensity, self-paced ergometer rowing.

3.4.2.3 Incremental Exercise Test

Standardized preparation prior to the incremental exercise test consisted of 5.0 min of self-selected stretching activities only—considered sufficient preparation for the initial low intensity stages of incremental exercise tests [216]. Participants were reminded of the individual incremental exercise test protocol to be followed, including the submaximal intensity and progressive maximum effort components, details of which are described below. Thereafter, the respiratory gas collection and HR recording equipment, prepared and checked in the same manner as described for the 2000 m rowing ergometer time trial above, was secured to the participant.

Participants performed a discontinuous incremental exercise test on the same Concept II, Model D rowing ergometer used for the 2000 m time trial, at the same standardized drag factor settings. Each test consisted of five or six submaximal intensity exercise stages, each lasting 4.0 min and each separated by 60 s of inactive recovery, followed by a final, progressive maximum effort stage. The first stage was completed at a power output of 100 W and the power output of subsequent stages increased by 30 to 50 W per stage in order to expose each participant to a range of submaximal exercise intensities. The size of the power output increases at each stage were individually determined based on participant performance in the 2000 m rowing ergometer time trial so as to base the submaximal exercise intensities on individual participant exercise capacity [304]. Specifically, power output for the stages of the incremental exercise test approximated 35%, 45%, 55%, 65%, 75% and 85% of the average power output maintained during the 2000 m time trial [14, 215]. The target stroke rate for the initial submaximal intensity exercise stage was 18 strokes·min^{-1} and was increased by 2 strokes·min^{-1} for each stage [51] to approximate the stroke rate typically used by the participants during rowing ergometer training involving these power output values. **Table 3.2** details the target power output for each participant for the five or six submaximal intensity stages of the incremental exercise test. Participants were encouraged to maintain a power output as close as possible to the target power output for each stage using visual feedback from the rowing ergometer computer. Average power output and average stroke rate during the final 2.0 min of each submaximal intensity exercise stage, obtained from the rowing ergometer computer, were recorded on a data sheet (Appendix E) for subsequent analysis.

Table 3.2: Target power output and stroke rate for each participant during five or six submaximal intensity stages of the incremental exercise test based on 2000 m rowing ergometer time trial performance.

Stage	**1**	**2**	**3**	**4**	**5**	**6**
Stroke	**18**	**20**	**22**	**24**	**26**	**28**
Intensity[#]	**35%**	**45%**	**55%**	**65%**	**75%**	**85%**
Participant	**Target power output (W)**					
1	100	150	200	250	300	350
2	100	150	200	250	300	350
3	100	140	180	220	260	300
4	100	150	200	250	300	
5	100	140	180	220	260	300
6	100	150	200	250	300	350
7	100	140	180	220	260	300
8	100	140	180	220	260	
9	100	140	180	220	260	
10	100	150	200	250	300	
11	100	140	180	220	260	
12	100	130	160	190	220	
13	100	130	160	190	220	
14	100	140	180	220		
15	100	130	160	190	220	250
16	100	130	160	190	220	250
17	100	130	160	190	220	250
18	100	140	180	220	260	
19	100	150	200	250	300	350
20	100	140	180	220	260	
21	100	140	180	220	260	
22	100	140	180	220	260	
23	100	140	180	220	260	
24	100	140	180	220	260	
25	100	150	200	250	300	

Note: * Expressed as strokes·min^{-1}.

[#] Expressed as approximate percentage of average power output achieved during the 2000 m rowing ergometer time trial.

Following the 60 s recovery period after the fifth or sixth submaximal intensity stage of the incremental exercise test, participants performed a final, progressive maximum effort exercise bout. This stage was initiated at the power output maintained for the last submaximal intensity of each participant's individual incremental exercise test protocol but participants were instructed to increase power output by 15 to 20 W every 30 s using a self-selected stroke rate until volitional exhaustion [36]. The highest average power output maintained over 30 s during this final stage was recorded as peak power output on a data sheet (Appendix E) for subsequent analysis. The VO_2, expressed in absolute terms ($L\cdot min^{-1}$) and relative to body mass ($ml\cdot kg^{-1}\cdot min^{-1}$) was measured continuously during the incremental exercise test, averaged every 10 s and recorded using the Schiller CS-200 Ergo-Spirometer. The highest HR and VO_2 measured over 30 s (three consecutive 10 s recordings) during the final, progressive maximum effort stage of the rowing ergometer incremental exercise test were recorded as maximum HR (HR_{max}) and maximum VO_2 (VO_{2max}) respectively [51]. Individual participant cardiorespiratory data files were marked on the exact start and end points of each stage of the incremental exercise test, exported to spreadsheet format and electronically stored for subsequent analysis. Following completion of the incremental exercise test the metabolic cart recording was stopped; participants were disconnected from the respiratory gas collection equipment and performed 5.0 to 10.0 min of low intensity, self-paced ergometer rowing.

3.5 Calculations and Derived Measures

3.5.1 Total Equivalent Oxygen Demand

The electronic spreadsheet files of cardiorespiratory data for each participant were analysed. For each submaximal intensity exercise stage of the incremental exercise test a steady-state was deemed to have been achieved if VO_2 displayed a relative plateau by varying less than 2.0 $ml\cdot kg^{-1}\cdot min^{-1}$ over the final 2.0 min of the stage [36, 209, 210, 229]. Only submaximal intensity exercise stages associated with steady-state VO_2 were included in the subsequent analysis. The average VO_2 over the final 2.0 min of each stage was recorded as the VO_2 associated with the corresponding average power output and these five or six coordinates were plotted for each participant individually to establish the VO_2-power output (VO_2-PO) relationship. These were checked for linearity to avoid inclusion of artificially high or low VO_2 values [141]. A minimum of five power output and associated VO_2 values were used to formulate each participant's VO_2-PO relationship. Linear regression yielded the slope and y-intercept of the VO_2-PO relationship. An example of the procedure employed for one participant is illustrated in **Figure 3.1**.

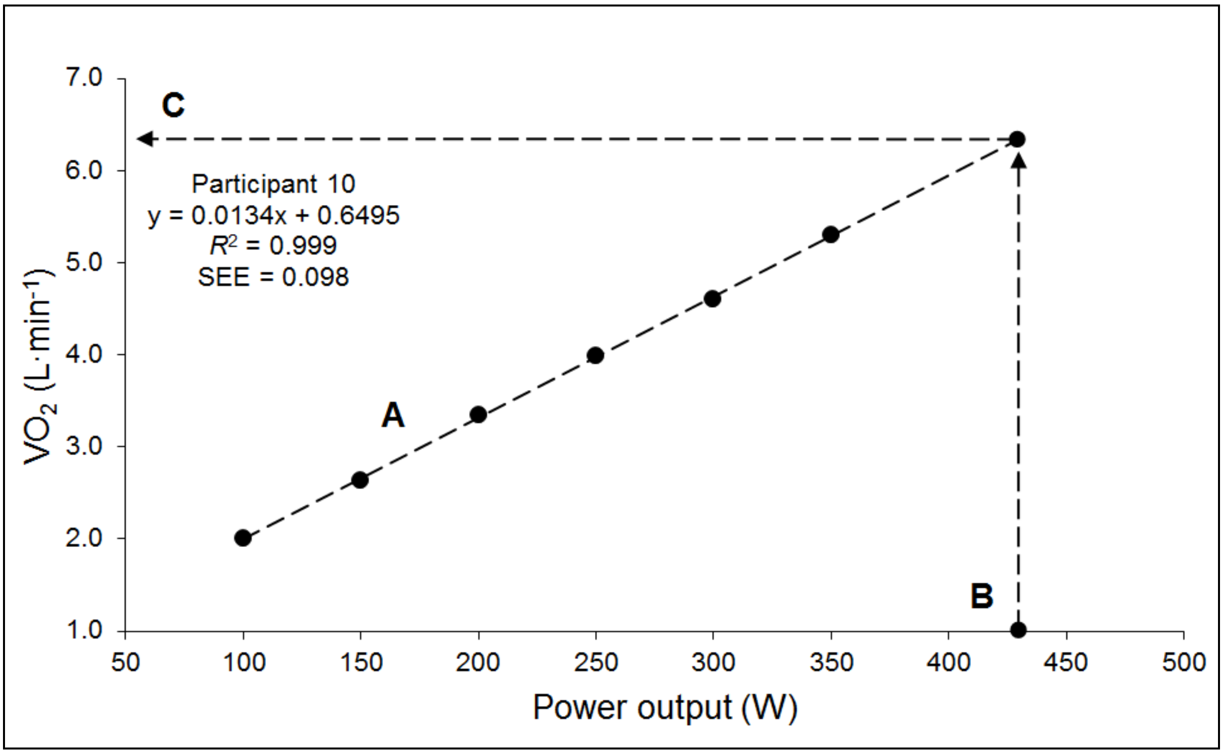

Figure 3.1: The oxygen uptake-power output regression equation obtained using data from the incremental exercise test for a single participant.

With reference to the symbols indicated in **Figure 3.1**, each participant's individual linear regression equation (A) was solved for the average power output achieved during the 2000 m rowing ergometer time trial (B) to forecast the equivalent VO_2 demand (L O_2 eq·min^{-1}) associated with the participant's time trial performance (C). Multiplying this rate by the duration of the maximum effort time trial yielded the total equivalent O_2 demand (L O_2 eq) of the 2000 m time trial performance [27]. Gross total equivalent O_2 demand included the VO_2 associated with resting biological work, while net total equivalent O_2 demand was obtained by subtracting resting VO_2, assumed to be 3.5 ml·kg^{-1}·min^{-1} [305] for each participant over the duration of the time trial.

3.5.2 Accumulated Oxygen Uptake

Using the electronic spreadsheet files of the cardiorespiratory data from the 2000 m rowing ergometer time trial, the volume (L) of O_2 utilized over each 10 s period during the time trial was calculated by correcting each 10 s recording of VO_2 (L·min^{-1}) to VO_2 per second and multiplying by the elapsed time (10 s). The cumulative volume of O_2 utilized—the accumulated O_2 uptake—

was then calculated by summing the O_2 utilization volumes for all the 10 s periods for the duration of the time trial. In cases where the 2000 m rowing ergometer time trial did not end exactly on a 10 s interval the O_2 utilization for the outstanding duration was portioned accordingly, as has been recommended [216]. Accumulated O_2 uptake values for the 2000 m rowing ergometer time trial were recorded as both gross and net quantities, with resting VO_2 assumed to be 3.5 $ml{\cdot}kg^{-1}{\cdot}min^{-1}$ [305].

3.5.3 Accumulated Oxygen Deficit

According to the method described by Medbø *et al*. [98], the accumulated O_2 deficit (AOD) was determined by subtracting the accumulated O_2 uptake during the 2000 m time trial from the total equivalent O_2 demand and was reported in both absolute (L O_2 eq) and relative (ml O_2 $eq{\cdot}kg^{-1}$) oxygen equivalent terms. Additionally, the AOD was recorded both unadjusted and adjusted for the aerobic energy contribution associated with the utilization of peripheral O_2 stores which is not reflected in the accumulated O_2 uptake obtained using respiratory gas analysis [98]. For the purpose of this study and based on the most suitable approximations available [136, 150] the contribution of these O_2 stores to the energy demand of the 2000 m rowing ergometer time trial was assumed to be 9.0 $ml{\cdot}kg^{-1}$ for each participant.

3.5.4 Relative Aerobic and Anaerobic Energy Supply

For each participant, aerobic energy system fractional contribution (%) during the 2000 m rowing ergometer time trial was calculated by dividing accumulated O_2 uptake during the time trial by total equivalent O_2 demand. The remaining fraction of the total equivalent O_2 demand was recorded as the anaerobic energy system fractional contribution. This procedure was followed using three sets of representations of the data described in the sections above, yielding three different expressions of the relative contribution of aerobic and anaerobic energy supply. Firstly, relative aerobic energy system contribution during the 2000 m rowing ergometer time trial was calculated by expressing gross accumulated O_2 uptake unadjusted for the desaturation of internal O_2 stores, as a percentage of gross total equivalent O_2 demand. Since the peripheral O_2 stores accounted for in the adjusted AOD in fact represent an aerobic contribution to ATP yield, that volume of O_2 utilization estimated for each participant was added to the accumulated O_2 uptake measured during the 2000 m rowing ergometer time trial before calculating the relative aerobic energy system contribution in the remaining methods, as has been recommended [216]. Secondly, the relative aerobic energy system contribution was calculated by expressing gross accumulated O_2 uptake adjusted for internal O_2 stores, as a percentage of gross total equivalent O_2 demand. Finally, relative aerobic energy system contribution was also calculated by expressing net accumulated O_2 uptake adjusted for internal O_2 stores, as a percentage of net total equivalent O_2 demand.

3.6 Data Analysis

For all data analysis procedures the SAS/STAT® statistical package version 9.01 (SAS Institute Inc., Cary, USA) was used. While principally a descriptive study, correlation and regression analysis methods were employed in this research project. Descriptive data calculated include the mean, standard deviation (SD), 95% confidence interval (CI) and range for all parameters measured and derived. For each participant, simple linear regression using the least squares method was used to calculate the line of best fit for the five or six coordinates representing the VO_2-PO relationship. The square of the interclass correlation coefficient, or common variance (R^2), was used to describe the adequacy of the VO_2-PO linear regression, while the standard error of the estimate (SEE) was used to indicate the precision of the regression lines [306]. Data distribution necessitated the use of non-parametric statistical methods for the correlation analysis [61]. Spearman's rank order correlation coefficient (rho) was calculated to assess the strength of the relationships between performance time in the 2000 m rowing ergometer time trial and the measures of aerobic and anaerobic energy supply during the trial, as well as between relative anaerobic energy supply and the general, anthropometric and rowing ergometer performance characteristics of the participants. Statistical significance was considered as $P < 0.05$ and rho values < 0.5, 0.5-0.8, and > 0.8 were interpreted as weak, moderate and strong respectively [306].

CHAPTER 4

RESULTS

4.1 Introduction

The results of this study are presented in the same order as the measurements described in Chapter 3 and the hypotheses presented in Chapter 1, with the descriptive results followed by the results of the correlation analysis. Unless otherwise stated, all results are presented as mean ± standard deviation (SD).

4.2 Descriptive Analysis

4.2.1 Participant Characteristics

General characteristics of the participants are listed in **Table 4.1**. Participants had an age of 21.0 ± 3.6 years, had been involved in formal training exclusively for rowing as a sport for 5.7 ± 3.4 years, and had personal best times (PBT) for a 2000 m rowing ergometer time trial within the two years prior to the study ranging from 5 min 59.7 s to 7 min 2.0 s. None of the participants indicated less than two years of exclusive rowing preparation. Nine of the twenty-five participants (36%) were in the national senior rowing team at the time of the study, having represented South Africa internationally in the season prior to the study, while the remaining sixteen (64%) were part of the national rowing squad. Descriptive anthropometric results include body mass (78.9 ± 7.6 kg), stature (185.2 ± 5.5 cm) and sum-of-seven skinfolds (53.6 ± 9.8 mm), and are listed in **Table 4.2**.

Table 4.1: General characteristics of participants (N = 25).

Variable	**Mean**	**SD**	**95% CI**	**Range**
Age (years)	21.0	3.6	19.6-22.4	18.0-28.0
Rowing training history (years)	5.7	3.4	4.3-7.1	2.0-14.0
2000 m rowing ergometer PBT (s)	393.3	19.1	385.8-400.8	359.7-422.0

Abbreviations: **SD** standard deviation; **CI** confidence interval; **PBT** personal best time.

Table 4.2: Anthropometric characteristics of participants (N = 25).

Variable	Mean	SD	95% CI	Range
Body mass (kg)	78.9	7.6	75.8-82.1	68.5-94.0
Stature (cm)	185.2	5.5	182.9-187.5	176.0-196.7
Sum-of-seven skinfolds* (mm)	53.6	9.8	49.6-57.7	35.1-74.2

Abbreviations: **SD** standard deviation; **CI** confidence interval.

Note: * Triceps, subscapular, biceps, supraspinale, abdominal, mid-thigh, and medial calf skinfolds.

4.2.2 2000 m Rowing Ergometer Time Trial

Performance time for the maximum effort 2000 m rowing ergometer time trial was 405.6 ± 20.5 s or 6 min 45.6 s with a range of 373.0 to 452.0 s, as indicated in **Table 4.3**. This was equivalent to an average power output of 341 ± 50 W, or approximately 92% of peak power output achieved in the incremental exercise test. Peak oxygen uptake (VO_{2peak}, 4.51 ± 0.54 $L \cdot min^{-1}$ or 57.2 ± 5.1 $ml \cdot kg^{-1} \cdot min^{-1}$) and peak heart rate ($HR_{peak}$, 191 ± 7 $b \cdot min^{-1}$) represented approximately 97% of both respective maximum values measured during the incremental exercise test.

Table 4.3: Performance measures, peak oxygen uptake and peak heart rate during the 2000 m rowing ergometer time trial (N = 25).

Variable	Mean	SD	95% CI	Range
Performance time (s)	405.6	20.5	397.1-414.0	373.0-452.0
Average power output (W)	341	50	320-362	243-431
Average stroke rate (strokes$\cdot min^{-1}$)	31.8	2.9	30.6-33.0	26.0-36.0
VO_{2peak} (absolute) ($L \cdot min^{-1}$)	4.51	0.54	4.29-4.73	3.70-5.55
VO_{2peak} (relative) ($ml \cdot kg^{-1} \cdot min^{-1}$)	57.2	5.1	55.1-59.3	47.4-65.0
HR_{peak} ($b \cdot min^{-1}$)	191	7	188-194	177-205

Abbreviations: **SD** standard deviation; **CI** confidence interval; **VO_{2peak} (absolute)** peak oxygen uptake in absolute terms; **VO_{2peak} (relative)** peak oxygen uptake expressed relative to body mass; **HR_{peak}** peak heart rate.

4.2.3 Incremental Exercise Test

The results from the incremental exercise test are listed in **Table 4.4**. Maximum oxygen uptake (VO_{2max}) for the group was 4.64 ± 0.54 $L{\cdot}min^{-1}$ or 58.9 ± 5.3 $ml{\cdot}kg^{-1}{\cdot}min^{-1}$ while maximum heart rate (HR_{max}) averaged 196 ± 6 $b{\cdot}min^{-1}$. The final progressive maximum effort stage of the incremental rowing ergometer test yielded a peak power output of 370 ± 48 W. The submaximal intensity oxygen uptake-power output (VO_2-PO) relationships for all twenty-five participants displayed common variances around the regression lines (R^2) of 0.981 or larger, while standard errors of the estimate (SEE) ranged from 0.022 to 0.125 $L{\cdot}min^{-1}$. The mean slope and y-intercept of the regression lines were 0.013 $L{\cdot}min^{-1}{\cdot}W^{-1}$ and 0.463 $L{\cdot}min^{-1}$ respectively, as illustrated in **Figure 4.1**.

Table 4.4: Peak power output, maximum oxygen uptake, maximum heart rate and characteristics of the oxygen uptake-power output relationship obtained from the incremental rowing ergometer test (N = 25).

Variable	**Mean**	**SD**	**95% CI**	**Range**
VO_{2max} (absolute) ($L{\cdot}min^{-1}$)	4.64	0.54	4.42-4.86	3.90-5.70
VO_{2max} (relative) ($ml{\cdot}kg^{-1}{\cdot}min^{-1}$)	58.9	5.3	56.7-61.1	48.6-67.9
HR_{max} ($b{\cdot}min^{-1}$)	196	6	194-199	182-206
Peak power output (W)	370	48	350-390	300-450
VO_2-PO slope ($L{\cdot}min^{-1}{\cdot}W^{-1}$)	0.013	0.001	0.013-0.014	0.012-0.015
VO_2-PO y-intercept ($L{\cdot}min^{-1}$)	0.463	0.102	0.423-0.503	0.300-0.657
VO_2-PO common variance (R^2)	0.995	0.004	0.993-0.996	0.981-0.999
VO_2-PO SEE ($L{\cdot}min^{-1}$)	0.061	0.028	0.050-0.072	0.022-0.125

Abbreviations: **SD** standard deviation; **CI** confidence interval; **VO_{2max} (absolute)** maximum oxygen uptake in absolute terms; **VO_{2max} (relative)** maximum oxygen uptake expressed relative to body mass **HR_{max}** maximum heart rate; **VO_2-PO** oxygen uptake-power output linear regression; **SEE** standard error of the estimate.

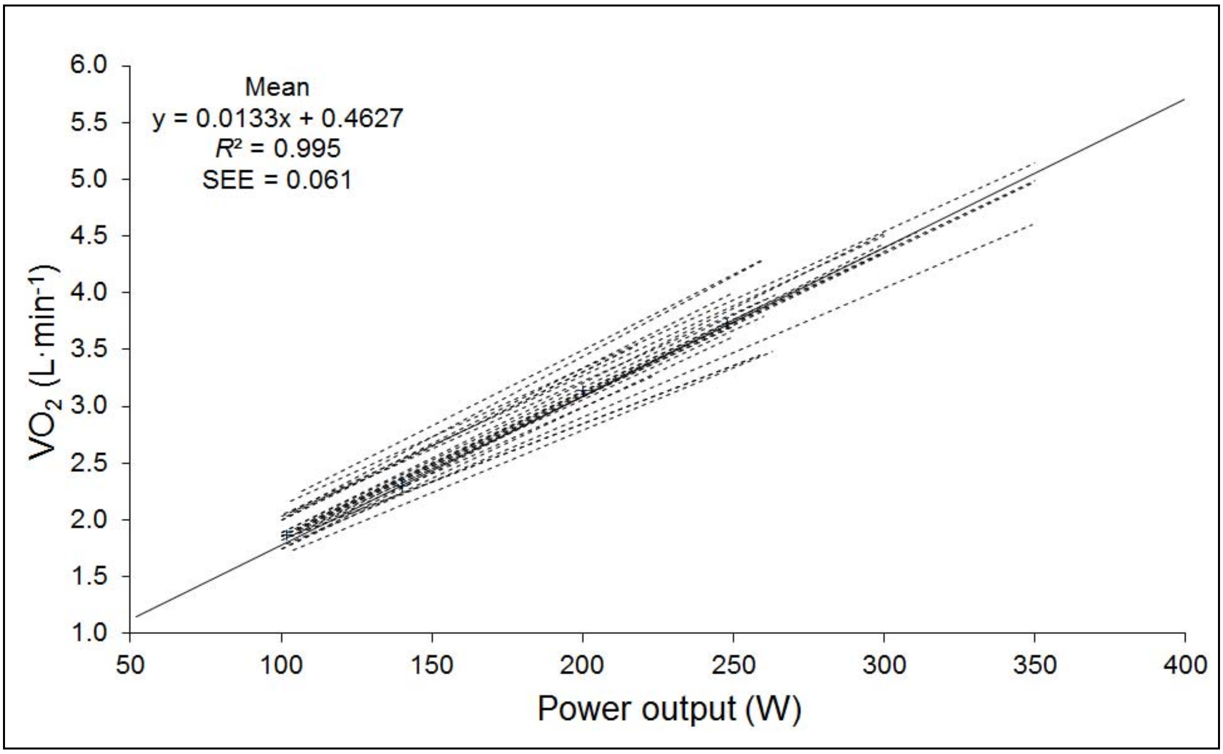

Figure 4.1: Oxygen uptake-power output regression lines established for each participant (broken lines) and the group mean (solid line) (N = 25).

4.2.4 Total Equivalent Oxygen Demand

Gross total equivalent oxygen (O_2) demand, the estimate of the overall energy demand of the 2000 m rowing ergometer time trial, averaged 33.55 ± 3.38 L O_2 eq for the group, while net total equivalent oxygen demand averaged 31.69 ± 3.33 L O_2 eq (**Table 4.5**).

Table 4.5: Total equivalent oxygen demand of the 2000 m rowing ergometer time trial, including (gross) and excluding (net) resting oxygen uptake* (N = 25).

Variable	**Mean**	**SD**	**95% CI**	**Range**
Gross O_2 demand (L O_2 eq)	33.55	3.38	32.16-34.95	27.92-39.94
Net O_2 demand (L O_2 eq)	31.69	3.33	30.31-33.06	26.11-37.89

Abbreviations: **SD** standard deviation; **CI** confidence interval.

Note: * Assumed to be 3.5 $ml\cdot kg^{-1}\cdot min^{-1}$ [305].

4.2.5 Accumulated Oxygen Uptake

The accumulated O_2 uptake—the sum total of oxygen utilization measured during the 2000 m rowing ergometer time trial performance—expressed in both gross and net terms averaged 26.74 ± 2.02 L and 24.88 ± 1.96 L respectively (**Table 4.6**).

Table 4.6: Accumulated oxygen uptake during the 2000 m rowing ergometer time trial, expressed as including (gross) and excluding (net) resting oxygen uptake* (N = 25).

Variable	**Mean**	**SD**	**95% CI**	**Range**
Gross accumulated O_2 uptake (L)	26.74	2.02	25.91-27.57	23.67-31.34
Net accumulated O_2 uptake (L)	24.88	1.96	24.07-25.68	21.79-29.30

Abbreviations: **SD** standard deviation; **CI** confidence interval.

Note: * Assumed to be 3.5 $ml{\cdot}kg^{-1}{\cdot}min^{-1}$ [305].

4.2.6 Accumulated Oxygen Deficit

Accumulated O_2 deficit (AOD) results, reported both unadjusted and adjusted for the desaturation of internal oxygen stores are listed in **Table 4.7**. The total equivalent O_2 demand, gross accumulated O_2 uptake and unadjusted AOD calculated for each participant are summarized in **Figure 4.2** along with the group means.

Table 4.7: Accumulated oxygen deficit during the 2000 m rowing ergometer time trial, expressed in absolute terms and relative to body mass, including (unadjusted) and excluding (adjusted) internal oxygen stores* (N = 25).

Variable	**Mean**	**SD**	**95% CI**	**Range**
AOD (absolute) (L O_2 eq) (unadjusted)	6.81	2.13	5.94-7.69	2.61-9.93
AOD (relative) (ml O_2 eq·kg^{-1}) (unadjusted)	85.9	24.7	75.7-96.1	33.7-122.9
AOD (absolute) (L O_2 eq) (adjusted)	6.10	2.10	5.28-6.92	1.91-9.08
AOD (relative) (ml O_2 eq·kg^{-1}) (adjusted)	76.9	24.7	67.2-86.6	24.7-113.9

Abbreviations: **SD** standard deviation; **CI** confidence interval; **AOD** accumulated oxygen deficit.

Note: * Assumed to be 9.0 $ml{\cdot}kg^{-1}$ [136, 150].

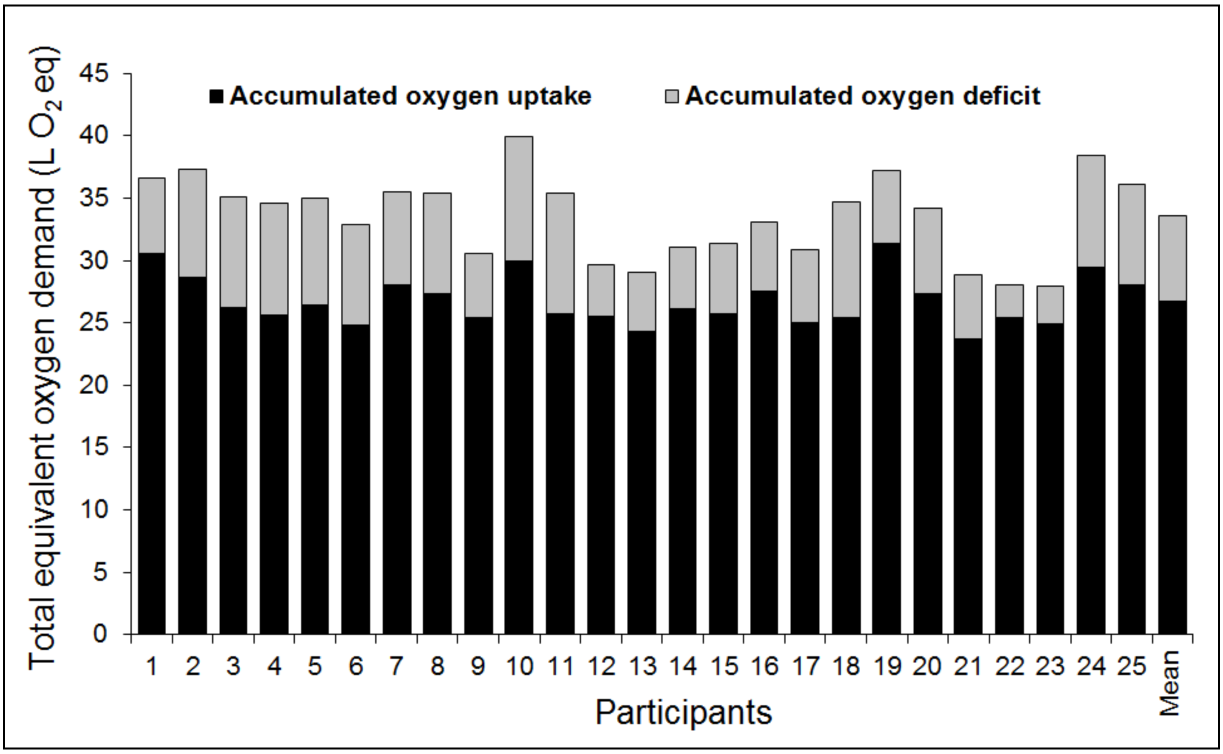

Figure 4.2: Individual participant and group mean total equivalent oxygen demand during the 2000 m rowing ergometer time trial, consisting of gross accumulated oxygen uptake and unadjusted accumulated oxygen deficit (N = 25).

4.2.7 Relative Aerobic and Anaerobic Energy Supply

The overall aerobic energy system fractional contribution during the 2000 m rowing ergometer time trial, calculated using three sets of data—including gross and net accumulated O_2 uptake both unadjusted and adjusted for the use of internal oxygen stores—approximated 80% to 82% of total energy demand (**Table 4.8**), with the remaining fraction attributed to anaerobic energy supply. **Figure 4.3** illustrates the relative contribution of aerobic and anaerobic energy supply during the 2000 m rowing ergometer time trial for each participant as well as the group mean, based on gross accumulated O_2 uptake unadjusted for the use of internal oxygen stores.

Table 4.8: Aerobic and anaerobic energy system relative contributions during the 2000 m rowing ergometer time trial (N = 25).

Variable	**Mean**	**SD**	**95% CI**	**Range**
Aerobic energy supply* (%)	80.0	5.0	78.0-82.1	72.7-90.7
Anaerobic energy supply* (%)	20.0	5.0	17.9-22.0	9.3-27.3
Aerobic energy supply$^{\#}$ (%)	82.2	5.1	80.2-84.1	74.9-93.2
Anaerobic energy supply$^{\#}$ (%)	17.8	5.1	15.9-19.8	6.8-25.1
Aerobic energy supply‡ (%)	81.1	5.3	79.0-83.2	73.3-92.7
Anaerobic energy supply‡ (%)	18.9	5.3	16.8-21.0	7.3-26.7

Abbreviations: **SD** standard deviation; **CI** confidence interval.

Note: * Calculated using gross accumulated oxygen uptake unadjusted for internal oxygen stores.

$^{\#}$ Calculated using gross accumulated oxygen uptake adjusted for internal oxygen stores.

‡ Calculated using net accumulated oxygen uptake adjusted for internal oxygen stores.

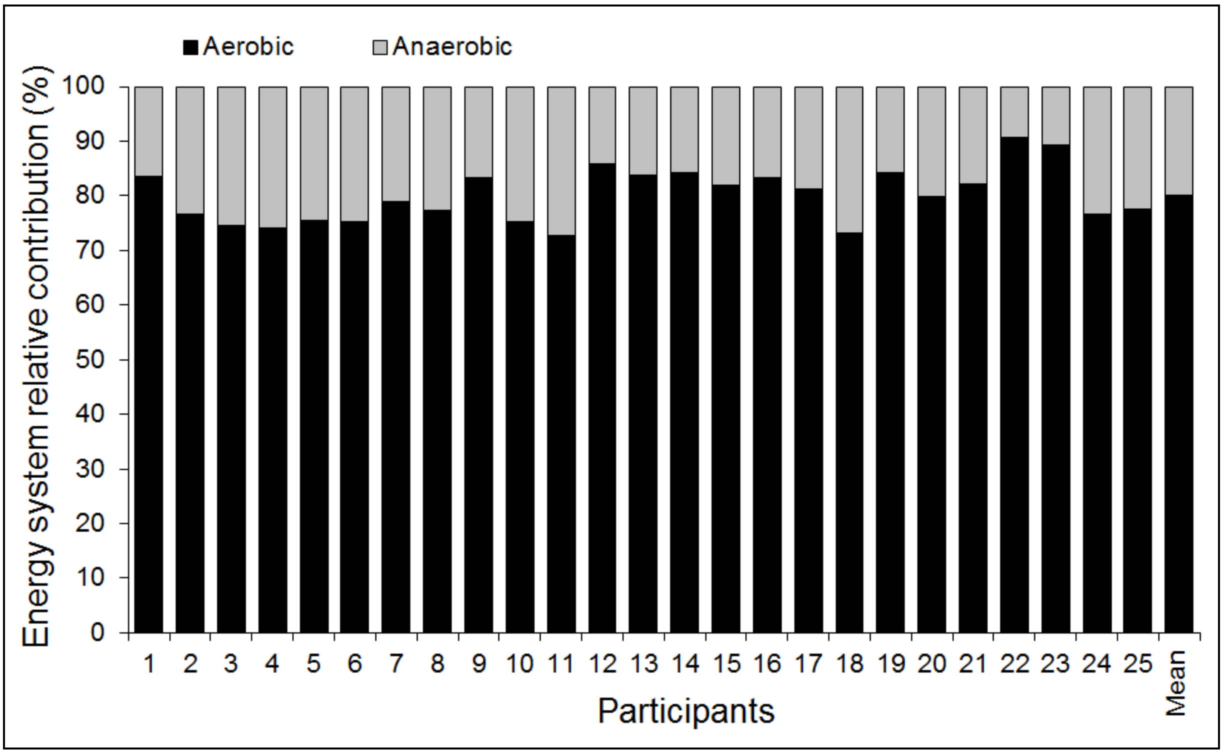

Figure 4.3: Individual participant and group mean relative aerobic and anaerobic energy system contribution during the 2000 m rowing ergometer time trial (N = 25).

4.3 Correlation Analysis

4.3.1 Performance Time, Participant Characteristics and Responses

Table 4.9 lists the results of the correlation analysis between 2000 m rowing ergometer performance time and participant general and anthropometric characteristics as well as rowing exercise test measures. Significant negative correlations were apparent with age, rowing training history, body mass, stature, VO_{2peak} in the 2000 m time trial, and both VO_{2max} and peak power output in the incremental exercise test. Of these, only VO_{2peak} and VO_{2max} expressed in absolute terms, as well as peak power output in the incremental exercise test, had strong relationships (rho < -0.8) with 2000 m rowing ergometer performance time. No significant correlations were found between 2000 m rowing ergometer performance time and sum-of-seven skinfolds or the VO_2-PO slope.

Table 4.9: Correlations between 2000 m rowing ergometer performance time and participant characteristics and rowing exercise test responses (N = 25).

Variable	**rho**[#]	***P*-value**
Age (years)	-0.725	< 0.001
Rowing training history (years)	-0.749	< 0.001
Body mass (kg)	-0.518	0.008
Stature (cm)	-0.554	0.004
Sum-of-seven skinfolds* (mm)	0.369	0.069
VO_{2peak} (absolute) ($L \cdot min^{-1}$)	-0.915	< 0.001
VO_{2peak} (relative) ($ml \cdot kg^{-1} \cdot min^{-1}$)	-0.581	0.002
VO_{2max} (absolute) ($L \cdot min^{-1}$)	-0.921	< 0.001
VO_{2max} (relative) ($ml \cdot kg^{-1} \cdot min^{-1}$)	-0.572	0.003
Peak power output (W)	-0.955	< 0.001
VO_2-PO slope ($L \cdot min^{-1} \cdot W^{-1}$)	0.132	0.530

Abbreviations: **VO_{2peak} (absolute)** peak oxygen uptake in the 2000 m rowing ergometer time trial expressed in absolute terms; **VO_{2peak} (relative)** peak oxygen uptake in the 2000 m rowing ergometer time trial expressed relative to body mass; **VO_{2max} (absolute)** maximum oxygen uptake in the incremental rowing ergometer test expressed in absolute terms; **VO_{2max} (relative)** maximum oxygen uptake in the incremental rowing ergometer test expressed relative to body mass.

Note: * Triceps, subscapular, biceps, supraspinale, abdominal, mid-thigh, and medial calf skinfolds.

[#] Spearman's rank order correlation coefficient.

4.3.2 Performance Time, Aerobic and Anaerobic Energy Supply

Correlations between 2000 m rowing ergometer performance time and measures of aerobic and anaerobic energy supply are shown in **Table 4.10**. Significant negative correlations were apparent with: gross and net total equivalent O_2 demand; gross and net accumulated O_2 uptake; AOD both unadjusted and adjusted for internal oxygen stores; and anaerobic energy fractional contribution during the rowing ergometer time trial. Significant positive correlations were found between 2000 m rowing ergometer performance and aerobic energy system contribution, irrespective of the method of calculation. However, only total equivalent O_2 demand in both gross and net representations, demonstrated a strong relationship (rho < -0.8) with performance time.

Table 4.10: Correlations between 2000 m rowing ergometer performance time and measures of aerobic and anaerobic energy supply (N = 25).

Variable	**rho†**	***P*-value**
Gross O_2 demand (L O_2 eq)	-0.815	< 0.001
Net O_2 demand (L O_2 eq)	-0.832	< 0.001
Gross accumulated O_2 uptake (L)	-0.630	< 0.001
Net accumulated O_2 uptake (L)	-0.626	< 0.001
AOD (absolute) (L O_2 eq) (unadjusted)	-0.707	< 0.001
AOD (relative) (ml O_2 eq·kg^{-1}) (unadjusted)	-0.582	0.005
AOD (absolute) (L O_2 eq) (adjusted)	-0.705	< 0.001
AOD (relative) (ml O_2 eq·kg^{-1}) (adjusted)	-0.582	0.005
Aerobic energy supply* (%)	0.548	0.005
Anaerobic energy supply* (%)	-0.548	0.005
Aerobic energy supply$^{\#}$ (%)	0.542	0.005
Anaerobic energy supply$^{\#}$ (%)	-0.542	0.005
Aerobic energy supply‡ (%)	0.542	0.005
Anaerobic energy supply‡ (%)	-0.542	0.005

Abbreviations: **AOD** accumulated oxygen deficit.

Note: * Calculated using gross accumulated oxygen uptake unadjusted for internal oxygen stores.

$^{\#}$ Calculated using gross accumulated oxygen uptake adjusted for internal oxygen stores.

‡ Calculated using net accumulated oxygen uptake adjusted for internal oxygen stores.

† Spearman's rank order correlation coefficient.

4.3.3 Relative Anaerobic Energy Supply and Participant Characteristics

The fractional contribution of anaerobic energy supply during the 2000 m rowing ergometer time trial showed significant positive associations with age, average power output and absolute VO_{2peak} during the time trial, as well as peak power output and absolute VO_{2max} during the incremental rowing test (**Table 4.11**), but correlations were typically weak. No significant relationships were evident between relative anaerobic energy supply and rowing training history, body mass, stature, sum-of-seven skinfolds, VO_{2peak} or VO_{2max} expressed relative to body mass, or the VO_2-PO slope.

Table 4.11: Correlations between relative anaerobic energy system contribution* and participant characteristics and rowing exercise test responses (N = 25).

Variable	**rho**‡	***P*-value**
Age (years)	0.501	0.011
Rowing training history (years)	0.393	0.052
Body mass (kg)	0.314	0.127
Stature (cm)	0.315	0.126
Sum-of-seven skinfolds# (mm)	-0.281	0.173
Average power output (W)	0.566	0.003
VO_{2peak} (absolute) ($L{\cdot}min^{-1}$)	0.402	0.047
VO_{2peak} (relative) ($ml{\cdot}kg^{-1}{\cdot}min^{-1}$)	0.236	0.257
VO_{2max} (absolute) ($L{\cdot}min^{-1}$)	0.439	0.028
VO_{2max} (relative) ($ml{\cdot}kg^{-1}{\cdot}min^{-1}$)	0.270	0.192
Peak power output (W)	0.537	0.006
VO_2-PO slope ($L{\cdot}min^{-1}{\cdot}W^{-1}$)	0.293	0.155

Abbreviations: **VO_{2peak} (absolute)** peak oxygen uptake during the 2000 m rowing ergometer time trial, expressed in absolute terms; **VO_{2peak} (relative)** peak oxygen uptake during the 2000 m rowing ergometer time trial, expressed relative to body mass; **HR_{peak}** peak heart rate during the 2000 m rowing ergometer time trial; **VO_{2max} (absolute)** maximum oxygen uptake during the incremental rowing ergometer test, expressed in absolute terms; **VO_{2max} (relative)** maximum oxygen uptake during the incremental rowing ergometer test, expressed relative to body mass.

Note: * Calculated using gross accumulated oxygen deficit, unadjusted for internal oxygen stores.

Triceps, subscapular, biceps, supraspinale, abdominal, mid-thigh, and medial calf skinfolds.

‡ Spearman's rank order correlation coefficient.

CHAPTER 5
DISCUSSION

5.1 Introduction

The primary objective of this study was to quantify the relative contribution of aerobic and anaerobic energy supply during a 2000 m maximum effort rowing ergometer time trial in elite male rowers, using the accumulated oxygen (O_2) deficit (AOD) method, with consideration for resting O_2 uptake (VO_2) and peripheral O_2 stores. A secondary objective was to determine the strength of the correlations between 2000 m rowing ergometer time trial performance and measures of aerobic and anaerobic energy supply during the time trial. The results of this study are discussed and interpreted in this chapter in order of these objectives. Limitations of the study which may have compromised the accuracy or generalizability of the results are acknowledged at appropriate points throughout this chapter.

5.2 Aerobic and Anaerobic Energy Supply during 2000 m Rowing Ergometry

The principal finding of this study was that aerobic energy supply dominates in contribution to total energy cost during a 2000 m rowing ergometer time trial, accounting for, on average, approximately 80-82% of total energy demand (**Table 4.8** and **Figure 4.3**). These results are comparable with those of previous studies investigating the aerobic and anaerobic energy supply during rowing, summarized in order of publication date in **Table 5.1**. The proportional aerobic and anaerobic energy contributions measured in the present study also compare well with the results of research in other exercise modalities employing tasks with similar performance durations. For example, studies on maximum effort cycling [129], kayaking and swimming [114] using the AOD method, and running using mathematical modelling [127], contend that performances lasting approximately 300 s are supported by relative aerobic energy supply contributions approximating 85% of total energy demand. Mean performance duration for the 2000 m rowing ergometer time trial in the present study was 406 s (**Table 4.3**). As Mäestu *et al*. [4] observed, rowing is frequently classified as a strength-endurance sport. Among several unique neuromuscular demands [12, 28, 264, 266] (**Section 2.3.6**), the muscular forces which produce and sustain rowing exercise are higher, and the contraction velocities lower than in other repetitive cyclic sports like running or cycling [255, 295]. This has prompted suggestions that higher anaerobic energy demands exist in rowing compared to maximum effort performances of similar duration in other exercise modalities [30]. The results described above appear to support this suggestion.

Table 5.1: Summary of studies investigating relative aerobic and anaerobic energy system contribution during ergometer rowing.

Authors [Reference]	**Participants**	**Protocol**	**Methodology**	**Relative aerobic energy system contribution (%)**	**Relative anaerobic energy system contribution (%)**
Hagerman *et al*. [29]	12 international level female rowers	4.0 min maximum effort rowing on an electrostatic rowing ergometer	Aerobic energy supply determined from net oxygen uptake; anaerobic energy supply determined by net oxygen deficit	70	30
Hagerman *et al*. [30]	310 international level male rowers	6.0 min maximum effort rowing on a Stanford mechanically braked rowing ergometer	Aerobic energy supply determined by net oxygen uptake; anaerobic energy supply determined by net oxygen debt during 30.0 min of recovery following exercise	70	30
Mickelson & Hagerman [31]	25 international level male rowers	15.0-18.0 min incremental intensity rowing on a Stanford mechanically braked rowing ergometer	Aerobic energy supply calculated as power output at anaerobic threshold expressed as a percentage of maximum power output during incremental exercise; anaerobic energy supply considered the remaining fraction	72	28

Table 5.1: (continued).

Authors [Reference]	**Participants**	**Protocol**	**Methodology**	**Relative aerobic energy system contribution (%)**	**Relative anaerobic energy system contribution (%)**
Droghetti *et al*. [32]	19 international level male rowers	6.0 min maximum effort rowing and 3 submaximal intensity stages of 3.0 min duration on a Gjessing friction-braked rowing ergometer	Aerobic energy supply determined from mean oxygen uptake; anaerobic energy supply determined from deficit between mean oxygen uptake and estimated total metabolic demand; total metabolic demand calculated by combining metabolic cost of power output and stroke rate measured independently	80	20
Russell *et al*. [35]	19 national level junior male rowers	2000 m maximum effort time trial (mean performance time ≈ 403 s) and 3 submaximal intensity stages of 5.0-7.0 min duration on a Concept II rowing ergometer	Aerobic energy supply determined from mean oxygen uptake; anaerobic energy supply calculated from oxygen deficit by subtracting mean oxygen uptake from estimated oxygen demand	84	16

Table 5.1: (continued).

Authors [Reference]	Participants	Protocol	Methodology	Relative aerobic energy system contribution (%)	Relative anaerobic energy system contribution (%)
Pripstein *et al*. [36]	16 female rowers ranging from club to international level	2000 m maximum effort time trial (mean performance time ≈ 450 s) and 4 submaximal intensity stages of 4.0 min duration on a Concept II rowing ergometer	Aerobic energy supply determined from accumulated oxygen uptake; anaerobic energy supply calculated from accumulated oxygen deficit as the cumulative difference between oxygen demand and oxygen uptake	88	12
Martin & Roberts [37]	4 national level female rowers	2000 m maximum effort time trial (mean performance time ≈ 441 s) on a Concept II rowing ergometer and extrapolation of an oxygen uptake-speed regression equation	Aerobic energy supply determined from accumulated oxygen uptake; anaerobic energy supply calculated from accumulated oxygen deficit as the cumulative difference between oxygen demand and oxygen uptake	89	11
de Campos Mello *et al*. [59]	8 club level male rowers	2000 m maximum effort time trial (mean performance time ≈ 402 s) on a Concept II rowing ergometer	Aerobic energy supply determined from net oxygen uptake; anaerobic energy supply calculated from fast component of excess post-exercise oxygen uptake and an energy equivalent of net post-exercise blood lactate concentration	84	16

Table 5.1: (continued).

Authors [Reference]	**Participants**	**Protocol**	**Methodology**	**Relative aerobic energy system contribution (%)**	**Relative anaerobic energy system contribution (%)**
Present study	25 national and international level male rowers	2000 m maximum effort time trial (mean performance time ≈ 406 s) and 5 or 6 submaximal intensity stages of 4.0 min duration on a Concept II rowing ergometer	Aerobic energy supply determined from gross and net accumulated oxygen uptake; anaerobic energy supply calculated from accumulated oxygen deficit adjusted and unadjusted for oxygen stores	80-82	18-20

The extent of dominance by aerobic energy supply during a maximum effort rowing race simulation demonstrated in previous studies, and corroborated by this study, is not surprising given the nature and magnitude of the responses measured for indices of absolute aerobic energy supply. Following a brief delay of approximately 20 s at the start of the rowing ergometer time trial, a rapid increase in VO_2 was observed (**Figure 5.1**), consistent with the crossover to predominantly aerobic delivery of ATP for continued skeletal muscle contractile activity reported to occur after only 15 to 30 s of maximum effort exercise [63]. Comparable responses have been reported elsewhere in studies involving maximum effort rowing and other exercise modalities [30, 36, 39, 85, 96, 97, 118, 128]. In a study by Mickelson & Hagerman [31], peak VO_2 (VO_{2peak}) measured during maximum effort 2000 m ergometer rowing was similar to maximum VO_2 (VO_{2max}) achieved during an incremental exercise test, a result corroborated by the present study (**Table 4.3** and **Table 4.4**). The VO_{2peak} values during the rowing ergometer time trial in the current study indicate that the rate of aerobic energy supply reached or exceeded approximately 97% of VO_{2max}.

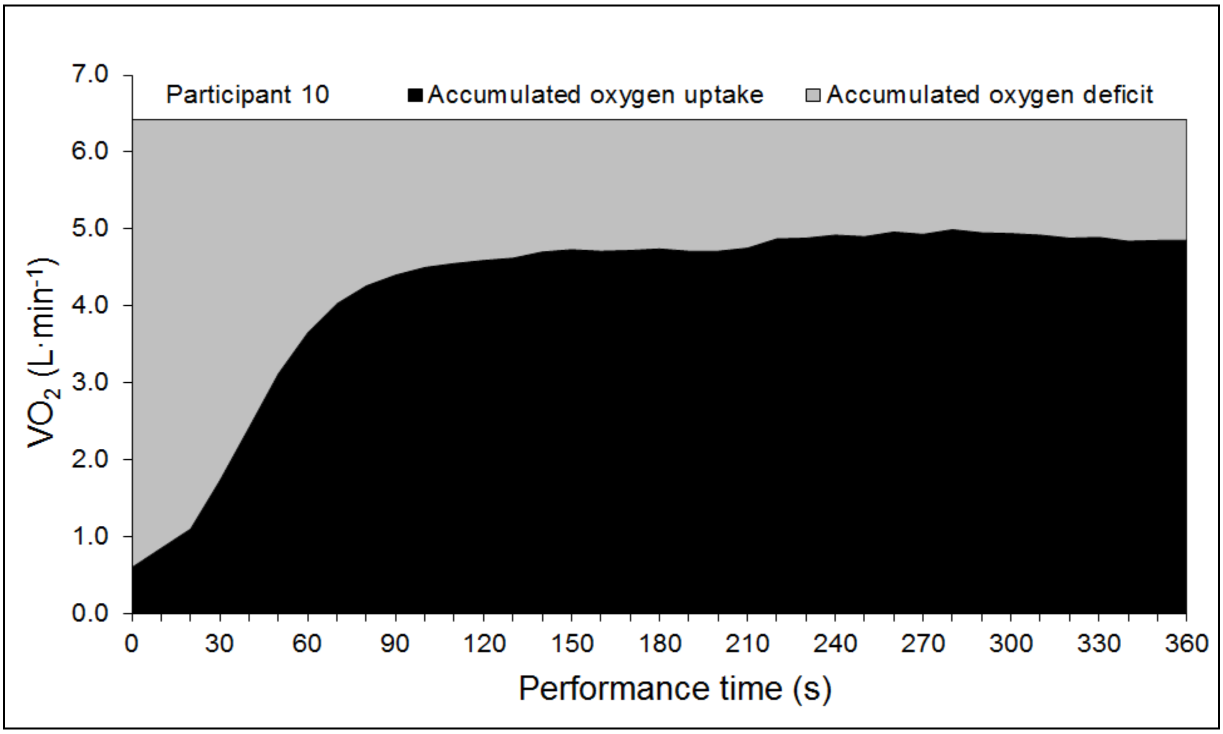

Figure 5.1: Accumulated oxygen uptake and accumulated oxygen deficit during the course of the 2000 m rowing ergometer time trial for a single participant.

However, while the nature and proportion of the response in aerobic energy supply measured in the present study is comparable with responses measured in rowers previously, the absolute indices of the rate of aerobic energy supply (VO_{2max} and VO_{2peak}) were lower than those for to elite male rowers studied by others [4, 10, 41, 42, 46, 266, 277, 307, 308]. For example, VO_{2max} in the present study (**Table 4.4**) averaged 4.64 $L{\cdot}min^{-1}$ (58.9 $ml{\cdot}kg^{-1}{\cdot}min^{-1}$) as opposed to the range of 5.00 to 6.60 $L{\cdot}min^{-1}$ (65.0-75.0 $ml{\cdot}kg^{-1}{\cdot}min^{-1}$) reported among world-class lightweight and heavyweight male rowers [30, 41, 266, 277, 295]. During the final 5.0 min of a 6.0 min maximum effort rowing ergometer test, Hagerman *et al*. [30] reported mean VO_2 values of 5.95 $L{\cdot}min^{-1}$, while the VO_{2peak} of participants in the present study averaged 4.51 ± 0.54 $L{\cdot}min^{-1}$ (**Table 4.3**). These differences may be partly explained by the relatively heterogenous participant group in the current study in respect of athlete calibre, training status and body size. On average, participants in this study were young, experienced and well-trained senior competitive rowers (**Table 4.1 to 4.4**), but individual variation within parameters was large. For example, rower representative level ranged from individuals who were competitive at national championship level to those with over a decade of international rowing experience. Further, nine participants (36%) were heavyweight rowers while sixteen (64%) were lightweight rowers, accounting for the wide range in measures of body size in this study (**Table 4.2**), and in all likelihood chiefly responsible for the range in absolute indices recorded for body size-dependent variables [10], including 2000 m rowing ergometer performance time, VO_{2peak}, peak power output, VO_{2max}, accumulated O_2 uptake, and AOD. Finally, although not entirely separable from body size when considering performance in rowing, based on 2000 m performance time and VO_{2max} values, the participants in the present study are likely to have been, on average, of a lower calibre and/or training status than the world-class rowers studied by others [30, 41, 266, 277, 295], potentially influencing the aerobic and anaerobic energy system contributions measured here.

Interestingly, cumulative aerobic energy supply, reflected by gross accumulated O_2 uptake, averaged 26.7 L (range: 23.7-31.3 L) (**Table 4.6**) in the present participant group, comparable to 30.9 L reported by Hagerman *et al*. [30] in their sample of world-class male rowers. The similarity in cumulative aerobic energy supply between the two studies despite considerable differences in VO_{2peak} values reported is likely explained by the longer performance time (by approximately 106 s) of the criterion rowing ergometer test in the current study (**Table 5.1**).

As early as 1925, Henderson & Haggard [11] remarked that "…*an oarsman exerts a power, which exceeds by 30 to 60 percent that afforded by the oxygen simultaneously absorbed, and incurs oxygen deficits of 4 to 8 litres or more*…". **Figure 5.1** demonstrates this phenomenon in illustrating the accumulated O_2 uptake and AOD during the 2000 m rowing ergometer time trial for a single participant in this study. As Xu & Rhodes [309] contended, during heavy to severe intensity exercise in which steady-state VO_2 is not achieved, the magnitude of the O_2 deficit continues to rise, or accumulate, until the termination of exercise. Hagerman *et al*. [29] appear to have published the first data on the size of the O_2 deficit incurred during ergometer rowing, reporting mean values of 4.40 L O_2 eq in female rowers during 4.0 min of exercise. But as Gastin [26] pointed out, AOD data for elite athletes and/or those in competitive training is generally scarce. For rowers, AOD values as high as 6.00 to 8.00 L O_2 eq [277] and 64.1 ml O_2 eq·kg^{-1} [141] have been reported, while in a review of rowing physiology, Hagerman [12] purported a range of 88.0 to 97.0 ml O_2 eq·kg^{-1} for AOD in experienced oarsmen. These values are comparable with the mean AOD (6.10 L O_2 eq or 76.9 ml O_2 eq·kg^{-1}) for the twenty-five participants in this study (**Table 4.7**), but are substantially larger than those reported by Russell *et al*. [35] (2.10 ± 1.42 L O_2 eq) for elite schoolboy rowers. However, since the corresponding value for female rowers has been measured as 3.50 ± 1.40 L O_2 eq [36] and 3.74 ± 2.05 L O_2 eq [37] during 2000 m rowing ergometer time trials lasting roughly 45 s and 35 s longer respectively, the validity of the AOD data presented by Russell *et al*. [35] appear questionable.

Interestingly, the AOD values recorded in the present study are higher than the 47.3 ml O_2 eq·kg^{-1} reported by Bangsbo *et al*. [141] in rowers performing a running test. In a review of AOD values reported in the research literature, Gastin [26] collated AOD results approximating a range of 2.00 to 7.50 L O_2 eq (30.0-100.0 ml O_2 eq·kg^{-1}) in trained and untrained participants across a variety of exercise modalities. Studies employing high intensity cycle ergometry have typically yielded AOD values of 30.0-80.0 ml O_2 eq·kg^{-1} [108, 119, 131, 207], 50.0 ml O_2 eq·kg^{-1} for sedentary individuals, and 70.0 ml O_2 eq·kg^{-1} for athletes trained in events dominated by anaerobic energy supply [78]. During high intensity running, Regan *et al*. [239] (79.9 ml O_2 eq·kg^{-1}), Medbø *et al*. [98] (90.0 ml O_2 eq·kg^{-1}) and Olesen [142] (100.0 ml O_2 eq·kg^{-1}) have reported particularly large AOD values when expressed in relative terms. The results of the investigations of AOD during maximum effort performances in rowing and in other exercise modalities are congruent with the data presented in this study, and together support the contention that the AOD is exercise task specific, with larger anaerobic energy supply in exercise task involving greater proportions of skeletal muscle mass [140-144].

The information presented above also highlights the extent of anaerobic energy supply in support of a high total energy demand during a 2000 m rowing ergometer time trial, even though relative anaerobic energy system contribution averaged just 18-20% in the current study (**Table 4.8**). Pripstein *et al*. [36] found that maximum AOD during short duration high intensity rowing ergometry was not significantly different to AOD measured during a 2000 m ergometer time trial, suggesting that anaerobic capacity may be taxed to a near-maximal degree during simulated rowing races. In competitive athletes, maximum effort exercise performances lasting 2.0 to 10.0 min are considered likely to elicit maximum absolute anaerobic energy yield, irrespective of total work completed or mean power output [134]. These contentions are supported by the fact that the AOD values reported in this study (**Table 4.7**) are among the highest published in scientific literature [9].

Nevertheless, regulating effort (pacing) and mechanical power output is inherent in maximum effort athletic events of intermediate duration [135, 136], and so the AOD measured in the present study represents anaerobic energy yield but not necessarily maximal anaerobic capacity. More specifically, since the 2000 m rowing ergometer time trial is not a constant power output time-to-exhaustion test, nor an all-out effort test, it cannot be assumed that the anaerobic capacity of the participants was fully exhausted, although it appears that this is at least possible in highly motivated, well-trained athletes performing maximum effort time trial formats of exercise [108, 110]. Additionally, the example from the present study illustrated in **Figure 5.1** shows that a large proportion of the AOD is accumulated within the first half of a 2000 m rowing ergometer time trial. How power output is regulated during maximum effort rowing tasks in order to manage the utilization of the theoretically finite anaerobic energy supply capacity while maintaining a competitive power output is worthy of investigation, as has been initiated using other exercise modalities [135, 136].

Returning attention to the results of previous research investigating relative energy system contributions during rowing, the studies in **Table 5.1** concur that maximum effort rowing performances are largely dependent on aerobic energy supply. All previous research efforts [29-32, 35-37, 59], as well as the present study, have arrived at aerobic energy system fractional contributions (70-90%) considerably larger during maximum effort rowing performances lasting 4.0 to 7.5 min than the values still reported (50-60%) in some modern textbook sources [16, 19]. The current results support the contention that traditional versions of relative energy supply models overestimate anaerobic contribution for maximum effort exercise tasks lasting longer than approximately 100 s [25], and that aerobic energy supply is of greater importance in maximum effort athletic events of intermediate duration than is still widely acknowledged [9, 63, 137].

Inspection of the results of the studies summarized in **Table 5.1** reveals that, within the dominance of aerobic energy supply recorded during maximum effort rowing performances suggested by research to date, a range approximating 20% exists between the results of individual studies (**Table 5.1**). As reviewed in detail in **Section 2.1.4** and **Section 2.2.8**, several factors are known or suspected to influence relative aerobic and anaerobic energy system contributions during maximum effort exercise. The possible role of absolute aerobic and anaerobic energy supply responses in affecting results in the present study have already been discussed independently above, as have the potential influences of participant body size and training status or athlete calibre. Additional explanations that may be pertinent to the interpretation of the results of the current study with respect to those of the studies listed in **Table 5.1** include the duration and relative intensity of the maximum effort criterion performance test, differences in AOD methodology employed, correction of measures for peripheral O_2 stores and resting VO_2, and the altitude of the study setting. These will each be discussed briefly.

Ignoring methodology, protocol and equipment differences between previous research efforts momentarily, considered from the perspective of differences in rowing performance time among studies listed in **Table 5.1**, results suggest that measurements made during slower and/or longer duration maximum effort rowing performances yield higher fractional aerobic energy system contributions. The position of aerobic (80-82%) and anaerobic (18-20%) proportional contributions calculated in the present study among those of previous studies is congruent with the position of the performance time of the criterion test imposed—approximately 406 s in the present study—among the corresponding performance times of the other studies. Owing to equipment and technological limitations at the time, early research efforts in this theme [29, 30, 32] imposed a 4.0 min (for females) or 6.0 min (for males) maximum effort test on a rowing ergometer to simulate 2000 m on-water rowing performance. Since contemporary ergometer rowing performance is described by the time taken to complete a set simulated distance [33], the results of more recent studies [35-37, 59, present study] employing a 2000 m time trial exercise format better represent the performance demands of rowing in terms of duration, relative intensity and pacing for most rowers [8, 33]. It is plausible that differences in the performance duration and format of the criterion rowing ergometer test imposed may therefore be responsible for at least some of the differences in relative energy system contributions measured in the studies summarized in **Table 5.1**.

The purpose of the 2000 m rowing ergometer time trial in this study was to impose a familiar, sport-specific, maximum effort, constant work (simulated distance) exercise task in order to elicit a representative physiological response and energetic demand typical of the relative intensity and duration of the task. While instructions and motivation were provided in an attempt to encourage a maximum effort during the test, participants in the current study generally, although not exclusively, did not produce personal best performances characteristic of real-world conditions (**Section 4.2**). Performance times for the 2000 m rowing ergometer time trial were, on average, approximately 3% slower than the participants' personal best times for the test. This is acknowledged as a constraint on the validity of the relative energy system contribution results calculated, since the relative intensity may not have been truly representative of a real-world race or performance trial. Laboratory exercise testing frequently relies on the assumption that athletes provide a maximum effort, but routinely fails to produce true personal best results [178-180]. It is curious that, of the published studies reporting aerobic and anaerobic energy system contributions during a 2000 m rowing ergometer time trial using the AOD method [35-37, 59], none have indicated the difference between performance time in the criterion time trial and personal best performance of the participants, making the influence of this phenomenon on the measurement of energy system involvement and relative contribution difficult to evaluate.

The most likely explanation for the differences in results between the studies summarized in **Table 5.1** is the different protocols and methodologies used in establishing energy system involvement and relative contribution. In 1983 Secher [254] observed that there was no simple way of accurately determining anaerobic energy supply during dynamic, whole-body exercise, and three decades on, this remains a frustration for exercise physiologists [23, 27, 217]. **Section 2.2** contains a brief review of published literature regarding the various techniques that have been employed in attempt to measure the anaerobic energy supply during exercise, most of which are known to yield inaccurate results. While all but one [31] of the studies in **Table 5.1** measured VO_2 to determine aerobic energy supply, the methods used to determine anaerobic energy supply, even among those employing the AOD concept, are far more dissimilar. A detailed appraisal of the AOD method, including the fundamental principles and limitations, suggested protocols, and validity and reliability data from the published literature, is contained in

Section 2.2.8. Briefly, the AOD method relies on the validity of the assumption that the energy demand associated with a maximum effort exercise bout can be determined from the relationship between power output during a series of submaximal intensity exercise bouts and the associated steady-state O_2 costs [9]. Differences in exercise protocols and calculation methods employed to establish the VO_2-power output (VO_2-PO) relationship make interpreting and comparing results between studies reporting relative aerobic and anaerobic energy system contributions during exercise difficult [126]. Unsurprisingly a recent review has reiterated the need for a standardized procedure for establishing the submaximal VO_2-PO relationship to improve the practical utility of the AOD method [27].

Assumptions about the mechanical efficiency of submaximal intensity and maximum effort exercise aside, characteristics of the VO_2-PO regression equations established in the AOD method describe the precision of estimating the total equivalent O_2 demand of the criterion exercise task [226], which in turn influences the magnitude of the AOD calculated, and hence the relative aerobic and anaerobic energy supply contributions. In the present study, the common variance (R^2) of the VO_2-PO linear regression equations averaged 0.995 ± 0.004 (**Table 4.4**), while the largest standard error of the estimation (SEE) for this relationship among the twenty-five participants was 0.125 $L{\cdot}min^{-1}$ (1.6 $ml{\cdot}kg^{-1}{\cdot}min^{-1}$), comparable with the corresponding measures of precision in those studies which have chosen to report this information using either rowing [32, 36] or other exercise modalities [98, 114, 124, 133, 161, 209, 210]. The slope of the VO_2-PO relationship differed by approximately 20% among the participants in the current study (**Figure 4.1**), reiterating the importance of using individually established VO_2-PO relationships to estimate total energy demand when using the AOD method rather than relying on common or assumed mechanical efficiencies.

The AOD calculated as the difference between total equivalent O_2 demand and accumulated O_2 uptake during an exercise task includes a small contribution from aerobic energy supply associated with the use of peripheral O_2 stores in oxidative phosphorylation, largely at the initiation of exercise, before systemic cardiorespiratory responses contribute to achieving a higher VO_2 [92]. While the existence and utilization of these stores has long been recognized [205], their size and extent of desaturation during exercise remains assumed, since direct measurement during dynamic, whole-body exercise is not possible [98]. Only a few of the studies that have employed the AOD method for estimating anaerobic energy supply during exercise appear to have considered the utilization of O_2 stores in calculations, and in those that have, reporting of values used in calculations is inconsistent [84, 98, 126, 136, 150, 231, 247]. Recommendations to practitioners and assumptions made in previous research for peripheral O_2 store utilization during exercise vary widely in nature and magnitude, including the use of fixed absolute values approximating 500 ml [24, 60, 205], fixed proportions (9-10%) of the AOD [145, 216], relative values of 2.3 $ml \cdot kg^{-1}$ [92] and 5.6 $ml \cdot kg^{-1}$ [126] in studies on cycle ergometry, or individually estimated values in ski skating exercise studies [136, 150]. Among those studies measuring anaerobic energy supply from AOD during rowing ergometry, it appears that none have corrected results for peripheral O_2 stores [29, 32, 35-37], while in one study this was considered part of anaerobic energy yield [299]. The extent of peripheral O_2 store size and desaturation during exercise would seem to be at least partially dependent on the size of the involved skeletal muscle mass, rendering considerations for body size and exercise modality important. Therefore in this study, the size of peripheral O_2 store utilization was assumed as the relative value of 9.0 $ml \cdot kg^{-1}$ based on the mean values estimated recently by Losnegard *et al*. [136, 150] for trained cross-country skiers during laboratory ski skating—a condition considered better approximating the extent of skeletal muscle involvement in trained rowers than the values used elsewhere [24, 60, 92, 126, 145, 205, 216]. Adjusting AOD for peripheral O_2 store desaturation yielded a smaller relative anaerobic energy supply contribution by approximately 2.0% (**Table 4.8**). While small, this difference approximates half the size of the reported precision of the AOD method for estimating anaerobic energy supply [98]. The size of the desaturation of peripheral O_2 stores should therefore be considered in research aimed at accurately measuring or interpreting changes in aerobic and anaerobic energy yields using the AOD method [145, 182, 216], and investigations should attempt to empirically determine the magnitude of this contribution during maximum effort rowing exercise.

Similarly, there remains a need to standardize and specify the correction or non-correction of total equivalent O_2 demand and/or accumulated O_2 uptake values for resting VO_2 in studies using these measures to calculate aerobic energy yield. **Table 5.1** indicates that, of seven previous studies using exercise VO_2 to calculate aerobic energy yield during maximum effort rowing performances, three [29, 30, 59] used net quantities while the others used either gross values or did not report the use of net or gross VO_2 [32, 35-37]. This may explain, in small part, the lower relative aerobic energy supply contributions (70%) reported by Hagerman & colleagues [29, 30] during maximum effort rowing performances in comparison with later studies. Using net rather than gross accumulated O_2 uptake yielded relative aerobic energy system contributions lower by approximately 1.0% for the 2000 m rowing ergometer time trial in this study, assuming a resting VO_2 of 3.5 $ml \cdot kg^{-1} \cdot min^{-1}$. Whether this difference is smaller than what may be considered meaningful remains to be investigated. The 2000 m time trial in the present study elicited average accumulated O_2 uptake values approximating 27.0 L (**Table 4.6**) during roughly 6 min 45 s of rowing (**Table 4.3**). The impact of using either gross or net total equivalent O_2 demand and/or accumulated O_2 uptake on relative aerobic and anaerobic energy yields calculated is likely to be greater in exercise tasks with a shorter performance duration, in which resting VO_2 represents a larger fraction of gross accumulated O_2 uptake. For accurate comparisons between results practitioners should clearly report the use of gross or net values in calculations when determining relative energy system contributions.

An interesting and potentially unique consideration in interpreting the results of the present study involves acknowledging the potential influence of altitude on the measurement of energy system contributions during exercise when using the AOD method. Russell *et al*. [35] calculated the relative aerobic (84%) and anaerobic (16%) energy supply contributions during a 2000 m time trial on a Concept II rowing ergometer in elite schoolboy rowers and, as in the present study, employed the AOD method. Notably, participants in their study displayed age (18.0 years), stature (187.0 cm), VO_{2max} (4.60 $L \cdot min^{-1}$) and 2000 m performance time (6 min 43 s) results sufficiently similar to those recorded in the present study to reasonably expect similar results for measures of aerobic and anaerobic energy supply during the time trial performances. Yet, as discussed earlier, Russell *et al*. [35] reported considerably lower AOD values (2.10 ± 1.42 L O_2 eq) than those observed in the present study (**Table 4.7**). Admittedly, comparisons of anaerobic energy supply measures between studies using the AOD method has been discouraged owing to the differences in protocols in use [126], and it is acknowledged that AOD differences between the two studies in question may well be the result of their dissimilar protocols (**Table 5.1**). However, the fact that the study by Russell *et al*. [35] was conducted at an altitude very near sea-level while the setting for the current study is at an altitude of 1340 m, invites speculation on this point.

The effect of different altitudes on the AOD measured during maximum effort rowing performance has yet to be investigated. However, in studies using all-out effort exercise formats in other modalities, it has been shown that acute reductions in inspired O_2 partial pressure attenuates exercise performance and VO_2 kinetics, while the absolute capacity for anaerobic energy supply may not be affected [98, 162-166]. Further, acclimation to increased altitude has been demonstrated to increase anaerobic capacity by approximately 12% [160]. As far as measures of aerobic energy supply are concerned, Wood *et al*. [310] demonstrated that even a modest altitude of 610 m significantly reduced VO_{2peak} during a 6.0 min rowing ergometer time trial in comparison to values measured at sea-level, despite no significant impact on total distance covered. With this evidence as background, it seems plausible that the altitude of the setting for the present study may be partly responsible for the large AOD values reported here in comparison to those described by Russell *et al*. [35], despite similar participant physical characteristics and rowing performance duration. This would consequently also explain the larger relative anaerobic energy supply contribution (18-20%) to the total energy demand of the 2000 m rowing ergometer time trial measured in the present study.

5.3 Relationships between Performance and Energy System Involvement

While several participant characteristics and responses demonstrated significant relationships with 2000 m rowing ergometer performance time in the current analysis, only a few showed correlations sufficiently strong to be considered sensitive discriminators between rowers of different performance abilities. Congruent with previous research [35, 36, 41, 43, 45, 47, 50, 51, 53, 55, 56], this study found significant correlations between 2000 m rowing ergometer performance time and indicators of the highest rate of aerobic energy supply during both incremental exercise (VO_{2max}) and during the time trial (VO_{2peak}) (**Table 4.9**). However, strong correlations existed only with VO_{2max} (rho: -0.921) and VO_{2peak} (rho: -0.915) expressed in absolute terms, and with peak power output (rho: -0.955) during incremental exercise. These results corroborate the observations of Secher *et al*. [41], who reported that the mean VO_{2max} within rowing crews, expressed in absolute but not relative terms, was strongly related to competitive rowing performance at an international regatta, despite the VO_{2max} and VO_{2peak} values of the participants in the current study being somewhat lower than those reported elsewhere for elite male rowers [4, 10, 41, 42, 46, 266, 277, 307, 308]. Thus, while absolute and relative expressions of the highest rate of O_2 utilization are related to 2000 m rowing ergometer time trial performance, those that perform better are typically able to achieve higher absolute rates of aerobic energy supply, thought to be largely a reflection of a larger body size [12, 264], as discussed below. Peak power output during incremental rowing ergometer exercise has also previously been shown to be a strong predictor of 2000 m ergometer performance [53]. Bourdin *et al*. [53] concluded that this was because peak power output represents an index of both physiological rowing capacity and rowing efficiency, and therefore permits the most robust differentiation of rowing ability in both heterogenous and homogenous groups. Similar results have previously been reported for running [311] and cycling [312].

This study yielded a non-significant correlation between rowing performance and the VO_2-PO slope, or delta efficiency (**Table 4.9**). While some studies have reported mechanical efficiency as a predictor of rowing performance [46], the relationship has been found to be weak by others [53]. Russell *et al*. [35] found no significant correlation between net efficiency and 2000 m rowing ergometer performance in elite schoolboy rowers. Delta efficiency is an index of individual submaximal intensity exercise efficiency [98]. As opposed to gross or net mechanical efficiency, delta efficiency represents the change in efficiency with each increment in submaximal intensity power output [220]. While the research evidence appears equivocal at present, the results of this study suggest that the relationship between energy expenditure and mechanical power output across a range of submaximal rowing intensities approximating 35-85% of average 2000 m time trial power output is not related to maximum effort time trial performance in a group of elite male rowers.

Body mass (rho: -0.518) and stature (rho: -0.554) showed significant, moderately strong correlations with time trial performance in this study (**Table 4.9**), consistent with what most studies measuring rower anthropometric characteristics have reported, even among similarly trained and experienced rowers [12, 35, 41, 44, 45, 55]. Larger individuals tend to have greater skeletal muscle cross-sectional areas and greater absolute capacity in several physiological parameters [12, 88]—distinct advantages when the requirement for a sustained, high power output in a 2000 m rowing performance is considered. By way of example, moderately strong relationships have been reported between VO_{2max} in absolute terms and body mass in rowers [254], illustrating one advantage that larger individuals have in rowing, in which body mass is supported [294]. Several physical attributes are also highly related to rower stature, including total lung capacity and heart size [12, 88]. While it is accepted that taller and heavier rowers tend to be more successful [264], some researchers have remarked that faster rowers also tend to have lower subcutaneous skinfold thickness and lower body fat contents than slower rowers [10, 28]. The sum-of-seven skinfolds recorded (53.6 ± 9.8 mm, **Table 4.2**) attests to the relative leanness of the participants in this study, but no significant relationship was present between time trial performance and sum-of-seven skinfolds (**Table 4.9**). These results suggest that within a sample of well-trained, relatively lean male rowers, the relationship between body fatness and 2000 m rowing ergometer time trial performance is weak.

In addition to the physical and physiological factors found to be associated with rowing ergometer performance in this study, rower age and experience—measured as years of specialized, dedicated rowing training—demonstrated moderately strong correlations with performance time (**Table 4.9**). Anecdotal reports suggest that the average rower reaching final races at international regatta level has been training for a minimum of four to five years [294]. The majority of Olympic-standard rowers are reportedly in their late twenties or early thirties [12]. The results of the present study suggest that experience and long-term preparation and participation may be important determinants of rowing performance.

Significant, moderately strong correlations (rho: -0.582 to -0.707) between 2000 m rowing ergometer performance time and AOD expressed in absolute and in relative terms, both unadjusted and adjusted for peripheral O_2 store utilization (**Table 4.10**), suggest that while anaerobic energy supply accounted for roughly one fifth of total energy demand, those with higher AOD values tended to perform better. This is in contrast to the findings by Russell *et al*. [35], who reported no significant correlation between AOD and 2000 m rowing ergometer performance in elite schoolboy rowers. It is possible that this difference in outcomes is a result of the stage of the competitive rowing season during which the studies were conducted. Exposure to higher intensity training involving greater anaerobic energy supply contributions typically increases as the rowing competition period approaches [4, 255, 266, 267]. The current study was conducted during the domestic competitive rowing season, while Russell *et al*. [35] describe their assessment period as pre-competition. The current results are consistent with those of several other studies which support anaerobic energy supply capacity as an important determinant of rowing performance [28, 36, 263].

The relationship between performance in rowing and total O_2 utilization, as described by the accumulated O_2 uptake in the current study, has been recognized for some time [30]. Some reviews suggest that average VO_2 during a rowing race may be among the best predictors of performance [12, 294]. As expected, significant, moderately strong correlations were evident between 2000 m rowing ergometer performance time and accumulated O_2 uptake expressed in both gross (rho: -0.630) and net (rho: -0.626) terms, supporting the conclusion that rowers delivering better performances do so with greater absolute aerobic energy supply [12, 264].

Arguably the most interesting finding from the correlation analysis in this study is that total equivalent O_2 demand was the only measure of energy supply that demonstrated significant and strong correlations (rho: > 0.8) with 2000 m rowing ergometer performance time (**Table 4.10**). Total equivalent O_2 demand is determined by the slope of the submaximal intensity VO_2-PO relationship and by the average power output associated with 2000 m time trial performance (**Figure 3.1**), and is necessarily the sum of absolute aerobic and anaerobic energy supply. As discussed above, the VO_2-PO slope (delta efficiency) yielded a non-significant relationship with performance time in this study (**Table 4.9**). Hence, it appears that total equivalent O_2 demand, established by the capacity to produce and maintain a high power output during rowing, and supported by the capacity for a high absolute energy supply—irrespective of the aerobic and anaerobic proportional contributions—is a better discriminator of rowing ergometer time trial performance than any single measure of aerobic or anaerobic energy supply.

To further investigate factors related to the proportional anaerobic energy supply during a maximum effort 2000 m rowing ergometer time trial, the strength of correlations between fractional anaerobic energy supply, based on calculations using gross AOD unadjusted for peripheral O_2 stores, and general, anthropometric and rowing ergometer performance characteristics of the participants, were evaluated (**Table 4.11**). The absence of a significant relationship with rowing training history, body mass, stature, sum-of-seven skinfolds, VO_{2max} and VO_{2peak} (both expressed in relative terms), and the VO_2-PO slope, indicate that experience, body size and leanness, indicators of endurance training status, and submaximal intensity ergometer rowing efficiency are likely not determining factors in relative anaerobic energy contribution during a maximum effort rowing performance. Significant correlations were evident between anaerobic energy supply contribution and mechanical power output achieved during both the time trial (average power output) and incremental rowing exercise test (peak power output), and the highest rates of aerobic energy supply expressed in absolute terms (VO_{2max} and VO_{2peak}), but these relationships were not strong (rho: 0.402 to 0.566). Nevertheless, these results support the contention that relative endurance fitness is a discrete construct from the capacity to supply energy anaerobically during a maximum effort intermediate duration exercise performance [144, 151-154, 156], but that interdependence exists between anaerobic energy supply during exercise and the absolute capacity for both high aerobic energy supply and power output [81]. The moderately strong correlation with age (rho: 0.501) is likely an artefact of the association between performance time and participant age in this sample of rowers.

Finally, it is acknowledged that the relatively small sample of convenience in the present study may restrict the generalizability of the results of both the descriptive and correlation analysis

[62]. While access to a larger number of rowers at national and international competitive levels was limited for this study, the sample size is comparable or larger than that in all but one of the studies on relative energy system contributions during rowing published to date (**Table 5.1**). Nevertheless, differences in sex, age and experience, body size, training status and performance capability represent the prime concerns when attempting to directly apply the current data regarding the relative contributions of aerobic and anaerobic energy supply during a 2000 m rowing ergometer time trial to other rowers. Future research should include these wider categories of the rowing population if broader generalizations are to be possible.

5.4 Summary

This study appears to be the first to have measured energy system contributions in national and international level senior male rowers during a maximum effort 2000 m rowing ergometer time trial on an air-braked ergometer using the AOD method, and to have examined the relationship between relative energy system contributions and time trial performance. Results confirm previous reports that aerobic energy supply during a 2000 m rowing ergometer time trial approximates 80-82% of estimated gross energy demand, supporting the first hypothesis of this study. Unsurprisingly, relative aerobic energy system contribution was lowest (80%) when calculated using gross accumulated O_2 uptake without considering peripheral O_2 store utilization. Correcting for resting VO_2 (3.5 $ml \cdot kg^{-1} \cdot min^{-1}$) and adjusting for desaturation of peripheral O_2 stores (9.0 $ml \cdot kg^{-1}$) respectively reduced (≈ 1%) and increased (≈ 2%) the aerobic energy supply fractional contribution calculated. It was further hypothesized that significant correlations existed between performance time and measures of both aerobic and anaerobic energy supply during the 2000 m rowing ergometer time trial. This was confirmed, but correlations were only moderately strong; as were the relationships between performance time and measures of rower experience, body size and measures of the capacity for aerobic energy supply expressed relative to body mass. By contrast, strong correlations between rowing performance time and peak power output, total equivalent O_2 demand, and absolute expressions of VO_{2max} and VO_{2peak} suggest that the fractional contributions of the energy systems may be superseded in importance by the capacity for a high total energy provision, dependent on high absolute rates of aerobic and anaerobic energy supply. Viewed in totality, the anthropometrical and physiological variables associated with 2000 m rowing ergometer time trial performance in this study suggest prioritizing the recruitment and preparation of rowers with the capacity to produce and maintain a high power output during rowing.

CHAPTER 6

CONCLUSIONS

6.1 Concluding Interpretations

Based on reports published to date [29-32, 35-37, 59], this study appears to be the first to measure relative energy system contributions in national and international level senior male rowers during a maximum effort 2000 m rowing ergometer time trial on an air-braked ergometer using the accumulated oxygen (O_2) deficit (AOD), and the first to examine the relationship between energy system contributions and time trial performance. The results confirm that aerobic energy supply dominates in contribution to total energy demand during a 2000 m rowing ergometer time trial, representing approximately 80% of total energy cost. In contrast to traditional textbook doctrine suggesting aerobic energy system fractional contributions in the region of 50-60% [16, 19], this study supports earlier [29, 30, 32] and more recent [35-37, 59] research reports which suggest a larger proportional dominance of aerobic energy supply in maximum effort rowing performances lasting 4.0 to 7.5 min. Peak pulmonary O_2 uptake (VO_{2peak}) and accumulated O_2 uptake measures confirm that a 2000 m rowing ergometer time trial demands a near-maximal rate of aerobic energy. Concomitantly, AOD values reported in this study are among the highest published in scientific literature, supporting the argument of extensive taxing of anaerobic energy supply capacity during competitive rowing [36]. Together, these results bear testament to the large total energy demand imposed by rowing exercise in general and the 2000 m rowing ergometer time trial specifically.

The results of this study also confirm strong relationships traditionally reported between rowing performance and physical and physiological characteristics of rowers, including measures of body size [12, 35, 41, 44, 45, 55] and endurance fitness [35, 36, 41, 43, 45, 47, 50, 51, 53, 55, 56]. The significant correlations between 2000 m rowing ergometer performance time and measures of both aerobic and anaerobic energy supply suggest that improved competitive performance is likely to occur if one or both of these capacities is improved. However, since strong correlations were found only between performance time and indicators of the capacity for total absolute energy expenditure (peak power output, VO_{2peak} and VO_{2max} in absolute terms, and total equivalent O_2 demand), it appears that the ability to produce and sustain a high power output during rowing, necessarily supported by high absolute rates of both aerobic and anaerobic energy supply, is the most important bioenergetic requirement for maximizing performance in a 2000 m rowing ergometer time trial. In addition, significant correlations between measures of aerobic energy supply capacity and fractional anaerobic energy system contribution support the concept of interdependence between aerobic and anaerobic energy supply during exercise [81].

6.2 Practical Applications

In contemporary high-performance sport programmes, exercise testing is performed to identify individual strengths and weaknesses within the context of event demands, monitor changes and evaluate the efficacy of preparation, provide objective feedback to athletes and coaches, indicate performance potential, assist in selection criteria and benchmarking, plot characteristics of elite performers and their responses to exercise, and/or produce guidelines for appropriate training interventions [3]. Within this framework the current study contributes information on the physiological responses and metabolic demands of rowing in general, and promotes a better understanding of the aerobic and anaerobic energy system involvement during 2000 m rowing ergometer time trial performances in particular.

The results of this study have practical application to coaches and sport scientists in the development, implementation and assessment of training programmes for elite rowers. Specificity of training is a principle regarded as essential for sporting success, and it requires prior evaluation of athlete characteristics and event demands [63]. Knowledge of the aerobic and anaerobic energy supply demands and relative contributions during an athletic event provides coaches with general guidelines on how to direct training time most effectively [125]. Based on the results of this study, designing training programmes which prioritize the development of improved aerobic energy supply capacity with a view to maximizing absolute power output and total energy supply during rowing would appear to be most specific to the energy system demands of a 2000 m rowing performance.

Appreciation of the energy system involvement and its association with performance in a 2000 m rowing ergometer time trial can also be used to better recognize important requirements for successful rowing performance. In this regard, attracting and managing rowers with the morphological and physiological attributes necessitated by the demand for high absolute energy expenditure during rowing would seem important for competitive success.

Finally, knowledge about aerobic and anaerobic energy supply and factors associated with superior performance in rowing illuminates the important physiological components or attributes that should be routinely monitored by exercise physiologists tasked with implementing and/or modifying the training programmes of competitive athletes [125]. While not novel in methodology or results, this study has broadened locally relevant rowing scientific knowledge which continues to be used to support coaching and scientific efforts aimed at improving the competitive performance of the South African national rowing squad.

6.3 Recommendations

The information gathered in this study has laid the foundation for further research related to the nature, extent and proportional involvement of aerobic and anaerobic energy supply during rowing, and several aspects remain to be addressed. Given that the absolute rate of energy expenditure is highly dependent on body size [10, 12, 147], it seems interesting to investigate whether the magnitude and pattern of energy system contributions during maximum effort rowing are similar across distinct categories of rowers—most obviously between heavyweight and lightweight rowers, and between male and female rowers—while accounting for absolute differences in performance duration. Differences in relative energy system contribution during maximum effort exercise are considered largely a product of task duration, relative intensity and modality [9]. While this study has yielded a cross-sectional profile of aerobic and anaerobic energy supply contributions in a sample of national and international level male rowers, it remains to be seen whether longitudinal monitoring of these profiles demonstrates significant changes in response to seasonal variations in training load and/or fitness status and the accompanying changes expected in performance trial duration and relative intensity.

Naturally, investigating such phenomena demands a method sensitive enough to detect meaningful changes in aerobic and anaerobic energy supply, and it has long been appreciated that improving the utility of the AOD method requires further research to establish its typical variation in homogenous groups of athletes within particular events [115]. In this regard, research to establish and improve the reliability and validity of the AOD method for rowing [226] should be built on. Furthermore, while the AOD and other methods of measuring anaerobic energy system involvement have been shown to yield similar results in running and cycling exercise tasks [217, 240, 241], it remains to be seen whether this holds true for rowing, which differs substantially from these exercise modalities in nature and extent of skeletal muscle involvement [10, 65, 253]. In light of the clear discrepancy between the results of this study and information widely purported in some textbook sources [16, 19], re-examining original research reports on energy system contributions in maximum effort athletic tasks with intermediate performance durations may be important to update recommendations to practitioners.

Finally, recent evidence from studies using other exercise modalities [109, 135] suggests merit in investigating the pattern of anaerobic energy supply utilized during rowing race simulations. In maximum effort athletic events with performance durations similar to on-water or simulated 2000 m rowing, distribution of the anaerobic energy supply resulting from power output regulation or pacing strategies may help to better understand and prepare for competitive events of this nature [23]. From the perspective of aerobic and anaerobic energy supply in support of skeletal muscle work, maximum effort 2000 m rowing exists in a proverbial grey zone of performance duration and cannot be classified as a short duration maximum intensity or prolonged duration submaximal intensity event. As a result, rowing is both intriguing and complex in its demands, and will likely continue to provide powerful inspiration for research into the physiological responses of high-performance rowers in this most severe form of physical activity.

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APPENDIX A

CONFIRMATION OF ETHICAL CLEARANCE

The Research Ethics Committee, Faculty Health Sciences, University of Pretoria comply with ICH-GCP guidelines and has US Federalwide Assurance. FWA 00002567, Approved dd 22 May 2002 and Expires 24 Jan 2009.
IRB 0000 2235 IORG0001762 Approved dd Jan 2006 and Expires 21 Nov 2008.

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0001

Date: 5/11/2007

PROTOCOL NO.	**Student 134/2007**
PROTOCOL TITLE	Energy system contribution to 2000-m rowing ergometry using the accumulated oxygen deficit.
INVESTIGATOR	**Person:** JR Clark **Phone:**012-3629800 x 1006 **Fax:** 012-4206099 **Cell:** 0826936785 **E-Mail:** peet.dutoit@up.ac.za jimmy.clark@up.a.c.za
DEPARTMENT	Physiology; University of Pretoria
STUDY DEGREE	M.Sc Physiology
SUPERVISOR	Dr P du Toit peet.dutoit@up.ac.za
SPONSOR	None.
MEETING DATE	31/10/2007

This Protocol has been considered by the Faculty of Health Sciences Research Ethics Committee, University of Pretoria on 31/10/2007 and found to be acceptable.

*Advocate AG Nienaber	(female)BA(Hons) (Wits); LLB; LLM (UP); Dipl.Datametrics (UNISA)
*Prof V.O.L. Karusseit	MBChB; MFGP (SA); M.Med (Chir); FCS (SA): Surgeon
*Prof M Kruger	(female) MB.ChB.(Pret); Mmed.Paed.(Pret); PhDd. (Leuven)
Dr N K Likibi	MB.BCh.; Med.Adviser (Gauteng Dept.of Health)
Snr Sr J. Phatoli	(female) BCur (Et.Al) Senior Nursing-Sister
*Dr L Schoeman	(female) Bpharm, BA Hons (Psy), PhD
*Prof J.R. Snyman	MBChB, M.Pharm.Med: MD: Pharmacologist
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Prof TJP Swart	BChD, MSc (Odont), MChD (Oral Path) Senior Specialist; Oral Pathology
*Dr A P van Der Walt	BChD, DGA (Pret) Director: Clinical Services of the Pretoria Academic Hospital
*Prof C W van Staden	MBChB; Mmed (Psych); MD; FTCL; UPLM; Dept of Psychiatry

Sommers

DR R SOMMERS; MBChB; M.Med (Int); MPhar.Med.
SECRETARIAT of the Faculty of Health Sciences Research Ethics Committee - University of Pretoria

* = Members attended the meeting on 31/10/2007.
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APPENDIX B

PARTICIPANT INFORMATION & INFORMED CONSENT

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RESEARCH STUDY TITLE

Energy system contribution to 2000 m rowing ergometry using the accumulated oxygen deficit

INTRODUCTION

We invite you to participate in a research study. This document will help you to decide whether you want to participate or not. Before you agree to take part you should fully understand what is involved. If you have any questions that this document does not fully explain, please do not hesitate to ask the investigator.

WHAT IS THE PURPOSE OF THE STUDY?

This research will study the body’s energy systems during a maximum effort 2000 m rowing ergometer time trial. The study aims to better describe the way the body provides energy for rowing and the requirements for superior rowing performance. As a competitive rower, you are a very important source of information about how the body works during rowing. This will assist sport scientists and coaches in better identifying rowers with the potential for success, better understanding the demands of rowing, and guiding training programmes to improve rowing performance.

WHAT PROCEDURES WILL BE FOLLOWED?

If you volunteer for this study you will assist us by providing information to achieve the aims above. You will be asked to complete a questionnaire about your rowing history, training and general health. You will undergo tests of body composition and rowing performance. The rowing tests will be conducted on a rowing ergometer while your breathing and heart rate are being recorded. One test will involve rowing at gradually increasing intensities. The other will be a maximum effort 2000 m time trial. If you have any concerns or questions about the testing, please ask the investigator to explain the procedures.

WHAT ARE THE POTENTIAL RISKS & DISCOMFORTS INVOLVED IN PARTICIPATING?

The risk involved in participating in this study is small. You will need to wear only shorts when we measure your body composition, and this may feel uncomfortable. These measurements will be made in a private, secure room by a male investigator only. The risk involved in the rowing ergometer tests should not be any greater than the exercise that you perform in your training sessions and in the time trials you have done on the rowing ergometer. You will be required to row inside a specially equipped laboratory, wearing a mask on your face to monitor your breathing and electrodes on your chest to monitor your heart rate. This may feel uncomfortable. The investigator is trained in the collection of your test data during exercise, and every effort will be made to minimize your discomfort. In the very unlikely event of a medical emergency during the exercise testing, the investigator is qualified in first aid and a doctor will be in the same building, so help will be available immediately. Since the effort we need you to provide during the rowing tests range from easy to maximum, you may experience some feelings of tiredness, pain, stiffness, or nausea (vomiting). The study will require about 3 hours of your time, split up into three 1-hour sessions on three separate days within the period of one week.

WHAT ARE THE BENEFITS OF PARTICIPATING IN THE STUDY?

In the short-term, you could benefit by the feedback you will receive on your body composition and rowing performance results, as well as recommendations on individual rowing training suggestions for improved performance. Indirectly and in the long-term, you may benefit when the information gained from this study is used to better monitor and plan your rowing training.

WHAT ARE YOUR RIGHTS AS A PARTICIPANT?

Your participation in this study is entirely voluntary. You can refuse to participate or stop at any time during the study without giving any reason. Your withdrawal will not affect you or your access to routine exercise testing and sport science support in any way.

WHAT ARE YOUR RESPONSIBILITIES AS A PARTICIPANT?

Information you have about your health, rowing history, nutrition or medication use may affect your safety in this study or the results of the study. You are responsible for fully and accurately disclosing this information in the participant questionnaire which will be provided to you and rapidly reporting any problems that may occur during the study which might affect your health or your ability to carry on with the study. You are responsible for following the participant instructions which will be provided to you, during this study.

HAS THE STUDY RECEIVED ETHICAL APPROVAL?

This study has received written approval from the Research Ethics Committee of the Faculty of Health Sciences at the University of Pretoria. A copy of the approval letter is available if you wish to have one.

CONFIDENTIALITY

The information that is obtained from your tests will be treated as strictly private and confidential. It will not be released or available to any person other than the investigators involved in the study and yourself. Your coach will be notified of your rowing test results if you so choose. The information will be used for statistical analysis, a research report and scientific presentations or publications, but your details will always remain anonymous.

COMPENSATION

Your participation is voluntary. No compensation will be provided for your participation and no contribution towards expenses (for example, travel costs) will be made.

INFORMATION & CONTACT DETAILS

You are free to ask the investigator any questions about the study, tests and instructions. If you have any concerns or questions, please ask us for further explanations. If you would prefer to make inquiries via telephone or email, the contact details of the investigator and supervisor can be found at the top of this document. Your time and cooperation as a participant in this study will be greatly appreciated.

FREEDOM OF CONSENT TO PARTICIPATE IN THIS STUDY

I have read, or had read to me in a language that I understand, the above information. I have had an opportunity to ask questions regarding the study and my involvement in it, and these have been answered to my satisfaction. The content and meaning of this information has been explained to me. I fully understand what I will be required to do as a participant in this study.

I therefore declare that I willingly participate in this project at my own risk, and have not withheld any information that may be of importance to the investigators or to my own safety. I am aware that I participate voluntarily and may withdraw from this study at any time if I so wish, without any prejudice or cost to myself.

I also grant the investigators permission to use my test results for scientific publication and/or presentation purposes, with my identity being kept anonymous.

I am free to request a summary of the research study outcomes at the end of the project if I so desire. I have received a signed copy of this informed consent agreement.

____
Name of participant

______________________ ______________________
Signature of participant Date

____
Name of investigator

______________________ ______________________
Signature of investigator Date

____
Name of witness

______________________ ______________________
Signature of witness Date

APPENDIX C

PARTICIPANT QUESTIONNAIRE

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RESEARCH STUDY TITLE
Energy system contribution to 2000 m rowing ergometry using the accumulated oxygen deficit

Accurate information regarding your personal contact details, rowing history, training status, recent diet and health status is important in protecting your safety and may affect the results of the study and your participation in the study. Please provide the following details honestly and comprehensively.

PERSONAL INFORMATION

NAME ____

DATE OF BIRTH ______________ AGE ______________ SEX ______________

PARTICIPANT NUMBER (to be completed by investigator) ______________________

CONTACT PERSON & INFORMATION IN THE EVENT OF AN EMERGENCY

NAME ____

RELATIONSHIP ______________ TELEPHONE NUMBER ______________

ROWING INFORMATION

NUMBER OF YEARS OF TRAINING EXCLUSIVELY FOR ROWING______________

ROWING CATEGORY & BOAT CLASS ______________________________

HIGHEST REPRESENTATIVE ACHIEVEMENT ______________________________

CURRENT COACH ______________ TELEPHONE NUMBER ______________

CONCEPT II ROWING ERGOMETER PERSONAL BEST TIMES WITHIN THE LAST 2 YEARS:

2000 m ______________ 5000 m ______________ 17000 m ______________

DIET & NUTRITIONAL SUPPLEMENTATION

ARE YOU CURRENTLY ON A MODIFIED NUTRITIONAL PLAN? ________________________________

IF YES, PROVIDE DETAILS ____

____

PLEASE LIST ANY NUTRITIONAL SUPPLEMENTS YOU ARE TAKING (NAME, DOSE)

____

ILLNESS

ARE YOU CURRENTLY SUFFERING FROM ANY ILLNESS? ___________________________________

IF YES, PROVIDE DETAILS (TYPE, SEVERITY) ____

____

HAVE YOU HAD ANY ILLNESS OR HEALTH PROBLEM IN THE LAST SIX WEEKS? ____________

IF YES, PROVIDE DETAILS (TYPE, SEVERITY) ____

____

DO YOU HAVE ANY CHRONIC HEART, LUNG OR METABOLIC DISEASE? __________________

IF YES, PROVIDE DETAILS (TYPE, SEVERITY) ____

____

INJURY

DO YOU CURRENTLY HAVE ANY INJURIES? ____

IF YES, PROVIDE DETAILS (TYPE, SEVERITY) ____

____

HAVE YOU HAD ANY INJURIES IN THE LAST SIX WEEKS? ________________________________

IF YES, PROVIDE DETAILS (TYPE, SEVERITY) ____

____

MEDICATION

ARE YOU CURRENTLY TAKING ANY MEDICATION? ____________________________________

IF YES, PROVIDE DETAILS (TYPE, DOSE) ____

____

HAVE YOU TAKEN ANY MEDICATION IN THE LAST SIX WEEKS? ______________________________

IF YES, PROVIDE DETAILS (TYPE, DOSE) ____

____

TRAVEL

HAVE YOU TRAVELLED WITHIN THE LAST SEVEN DAYS? ___________________________________

IF YES, PROVIDE DETAILS (MODE, DURATION, VENUES) ___________________________________

____

CURRENT TRAINING, RECOVERY & FITNESS

EVALUATE YOUR CURRENT TRAINING (FREQUENCY, DURATION, INTENSITY, MODE)

____

____

EVALUATE YOUR MOTIVATION FOR PERFORMING INTENSE EXERCISE WITHIN THE NEXT 7 DAYS (POOR, FAIR, GOOD, EXCELLENT)

____

EVALUATE YOUR PHYSICAL CAPACITY FOR PERFORMING INTENSE EXERCISE WITHIN THE NEXT 7 DAYS (POOR, FAIR, GOOD, EXCELLENT)

____

ADDITIONAL INFORMATION THAT MAY INFLUENCE YOUR EXERCISE TEST RESULTS

____

DECLARATION

I, ____ (print full name), have given true and complete information to the best of my knowledge in this questionnaire. I hereby give the researchers permission to use this information, with my anonymity being ensured.

______________________________	______________________________
Signature of participant	Date

APPENDIX D

PARTICIPANT INSTRUCTIONS

UNIVERSITEIT VAN PRETORIA
UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA

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PARTICIPANT INSTRUCTIONS

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Supervisor

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To improve the accuracy of your test results in the study, the following standardized preparations should be adhered to during the study.

TRAINING

Ensure that no severe exercise, new exercise or resistance training exercise is performed in the 24 hours prior to any testing. A day of testing should not include any training before testing. You may continue with scheduled training during the study period but perform only steady endurance rowing training the day before testing in the form of 90 min rowing, 12 km, stroke rate 18-22.

ENVIRONMENT

Avoid exposing yourself to dramatic changes in your environmental conditions in the days preceding any testing. Unaccustomed exposure to different environmental temperatures, pressures, or travel should be limited. For example, refrain from sauna, long drives or air travel, or altitude changes before and during the testing period.

EQUIPMENT

You must bring the correct exercise gear and wear light and comfortable clothing. Clothing should permit freedom of movement and appropriate test procedures. A typical tri-suit used for rowing is ideal, along with shorts, t-shirt, towel, water bottle, shoes to row on the ergometer with, and a tracksuit.

HEALTH

You must be in good health on each day of testing, and fully recovered from any previous injuries or illnesses. Anything which might limit maximum effort in an exercise test must be mentioned to the investigator and reported in the participant questionnaire, and may result in your exclusion from the testing and/or the study. Ensure good quality sleep the night before all testing. Where applicable, the normal use of prescription medications should be followed as recommended by your doctor.

NUTRITION

In the 24 hours preceding a test, avoid drinking any alcohol. On the day of testing, avoid caffeine containing substances, like tea, coffee, cola drinks, and chocolate. No substances should be taken in an attempt to enhance physical performance. You should be well hydrated throughout the day of testing and the day prior to testing by drinking sufficient fluid. Good quality nutrition is essential. Avoid any unaccustomed food during the period of the study. Ensure that meals on the days prior to and days of testing are nutritionally balanced and familiar. The last meal before testing should be a mixed one, around 3 hours before the strenuous exercise tests. Thereafter, only take water if desired. The examples below provide a guideline for nutritional timing and content on the day of testing.

APPROXIMATE TEST TIME	NUMBER AND TIMING OF MEALS
09H00	Early breakfast around 06H00
14H00	Breakfast, snacks as usual, lunch around 11H00
16H00	Breakfast, snacks as usual, lunch around 13H00

Typical breakfast: 1 bowl cereal with 1 cup milk; 1 English muffin with spread; 1 glass of fruit juice
Typical snack: 2 pieces of fruit; 1 cereal bar or 1 energy bar
Typical lunch: 1 chicken breast; 2 cups rice or pasta; 1 glass fruit juice

APPENDIX E

DATA RECORDING FORM

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PARTICIPANT NUMBER ___________________

TEST SESSION 1

DATE _______________TIME _______________

ANTHROPOMETRY

BODY MASS		kg	STATURE		cm
SKINFOLD THICKNESS	TRICEPS	mm	SKINFOLD THICKNESS	ABDOMINAL	mm
	SUBSCAPULAR	mm		MID-THIGH	mm
	BICEPS	mm		MEDIAL CALF	mm
	SUPRASPINALE	mm		**SUM-OF-7 SKINFOLDS**	mm
TEST NOTES					

ROWING ERGOMETER 2000 m TIME TRIAL

DRAG FACTOR	**PERFORMANCE TIME (s)**	**AVERAGE POWER OUTPUT (W)**	**AVERAGE STROKE RATE (strokes·min^{-1})**
TEST NOTES			

TEST SESSION 2

DATE ______________ TIME ______________

ROWING ERGOMETER INCREMENTAL EXERCISE TEST

STAGE	**CUMULATIVE TIME (min)**	**DRAG FACTOR**	**TARGET STROKE RATE (strokes·min^{-1})**	**TARGET POWER OUTPUT (W)**	**AVERAGE STROKE RATE (strokes·min^{-1})**	**AVERAGE POWER OUTPUT (W)**
1	4		18			
2	9		20			
3	14		22			
4	19		24			
5	24		26			
6	29		28			
MAX	34		30+			
TEST NOTES						