

PETER W. HOCHACHKA

GEORGE N. SOMERO

Biochemical Adaptation

PETER W. HOCHACHKA

GEORGE N. SOMERO

Biochemical Adaptation

Princeton University Press

Princeton, New Jersey

Copyright © 1984 by Princeton University Press

Published by Princeton University Press, 41 William Street,
Princeton, New Jersey 08540

In the United Kingdom: Princeton University Press, Guildford,
Surrey

All Rights Reserved

Library of Congress Cataloging in Publication Data will be
found on the last printed page of this book

ISBN 0-691-08343-6 (cloth)

ISBN 0-691-08344-4 (paper)

This book has been composed in Lasercomp Times Roman

Clothbound editions of Princeton University Press books are
printed on acid-free paper, and binding materials are chosen for
strength and durability. Paperbacks, although satisfactory
for personal collections, are not usually suitable
for library rebinding

Printed in the United States of America by Princeton
University Press, Princeton, New Jersey

PREFACE

One of the great accomplishments of biochemistry and molecular biology has been the elucidation of many of the major unifying principles and mechanisms that serve as the foundations of all living systems. Common mechanisms of energy transformation, catalysis, and the coding and processing of genetic information testify to the unity of life at the molecular level. While no one can deny these triumphs of reductionist approaches to biology, these insights into unifying principles of biochemical design in living systems seem to offer relatively few direct answers to a question of central importance to many biologists: How to account for the mechanisms underlying the immense diversity of organisms? What are the fundamental ways in which the basic biochemical structures and functions of living systems are adaptively modified to allow organisms to exploit the full range of natural environments and to maintain the radically different modes of life we see in nature?

The question of how a set of common mechanisms are extended into uncommon and diverse contexts is not new. Decades ago a similar gap existed between the fields of comparative anatomy and physiology. This gap was bridged by the concept of adaptation, and it is our belief that the concept of adaptation can be extended to the molecular level to effect a bridge between the observations of universal molecular mechanisms, on the one hand, and extreme biological diversity, on the other hand. Thus, the focus of our book is on the ways in which the ubiquitous molecular structures of organisms are modified to permit organisms to thrive in such diverse environments as the polar regions, deserts, and the deep sea, and to achieve modes of living that may involve major changes in type and quantity of nutrients available and in the oxygen that is present to support respiration.

In developing the central theme of biochemical adaptation we have selected examples for study that strike us as providing especially clear illustrations of the fundamental strategies of adaptation at the biochemical level. Our scope of treatment is not encyclopedic. Instead, we have focused on topics for which there either are numerous data, which allow a detailed analysis to be achieved, or where the basic

phenomenology is so interesting that, despite a lack of large numbers of data, it seemed to us worthwhile to draw questions of potential interest to the readers' attention. Our hope is that the examples we have chosen will be exciting and will provide the reader with an impetus to examine other, less well-studied problems in biochemical adaptation.

Our indebtedness to those whose efforts have helped make this book possible is a pleasure to acknowledge. At the top of the list are the students and postdoctoral scholars who have given us the type of stimulation that has kept our enthusiasm for this writing project, and for research per se, at a high pitch. P.W.H. wishes to express particular thanks to the students and postdoctoral fellows contributing to the current fermentations in his laboratory: H. Abe, J. Ballantyne, M. A. Castellini, G. P. Dobson, J. F. Dunn, B. Emmett, R. Foreman, C. J. French, U. Hoeger, T. P. Mommsen, B. J. Murphy, W. Parkhouse, E. A. Shoubridge, and R. Suarez. Earlier students who have continued to influence the thinking and work in P.W.H.'s laboratory include J. Baldwin, H. Behrisch, J.H.A. Fields, H. Guderley, M. Guppy, T. P. Moon, T. Mustafa, T. Owen, J. Storey, and K. B. Storey. In addition, P.W.H. wishes to acknowledge his numerous colleagues around the world who have made the entire enterprise all the more exciting and who on occasion have combined the adventures of intellect with the adventures of scientific expedition.

G.N.S. wishes to express his gratitude to past and present members of the Scripps Institution of Oceanography High Pressure Zone Laboratory: L. Borowitzka, R. D. Bowlus, M. A. Castellini, B. J. Davis, K. A. Dickson, V. Donahue, J. G. Duman, H. Felbeck, S. L. French, E. Golanty, J. E. Graves, G. S. Greaney, S. C. Hand, K. H. Hoffmann, D. Kramer, G. Lopez, P. S. Low, M. S. Lowery, J. Malpica, E. Pfeiler, M. A. Powell, S. J. Roberts, J. F. Siebenaller, K. M. Sullivan, R. R. Swezey, P. J. Walsh, P. H. Yancey, and M. Yacoe. Stimulating discussions of many of the ideas in this book with Drs. J. J. Childress, M. E. Clark, and F. N. White also have been invaluable.

Neither this project nor much of our work described in it could have been achieved without support from NSERC and the Canadian Heart Foundation (P.W.H.) and the NSF and NIH (G.N.S.). Special thanks are given by P.W.H. to the Australian Department of Science and Technology for support via a Queen's Senior Fellowship.

Finally, we wish to emphasize that the task of preparing a book transcends the generation of ideas. The manipulation of manuscripts and figures, while the primary responsibility of the authors, could

not have been achieved effectively without the enormous efforts of Ms. Leslie Borleski, Ms. Kathy Lingo, and Ms. Cecelia Ross. And, lastly, both authors acknowledge the emotional support of the members of the Laika family tree.

Peter W. Hochachka

Vancouver, British Columbia

George N. Somero

La Jolla, California

LIST OF ABBREVIATIONS

Common Metabolites

AMP, ADP, ATP	adenosine 5'-mono-, -di-, -triphosphate
cAMP	3',5'-cyclic AMP
ArgP	arginine phosphate
CMP, CDP, CTP	cytidine 5'-mono-, -di-, -triphosphate
CoA	coenzyme A
Cr, CrP	creatine, creatine phosphate
DG	diglyceride
DHAP	dihydroxyacetone phosphate
DNA	deoxyribonucleic acid
2,3 DPG	2,3 diphosphoglyceric acid
FAD ⁺ , FADH	flavin adenine dinucleotide, and its reduced form
F6P	fructose 6-phosphate
F1,6BP	fructose 1,6-bisphosphate
F2,6BP	fructose 2,6-bisphosphate
G3P	glyceraldehyde 3-phosphate
G6P	glucose 6-phosphate
GMP, GDP, GTP	guanosine 5'-mono-, -di-, -triphosphate
imid	imidazole
IMP, IDP, ITP	inosine 5'-mono-, -di-, -triphosphate
KGA	ketoglutarate
MG	monoglyceride
NAD ⁺ , NADH	nicotinamide adenine dinucleotide, and its reduced form
NADP ⁺ , NADPH	nicotinamide adenine dinucleotide phosphate, and its reduced form
P5C	pyrroline-5-carboxylate
PEP	phosphoenolpyruvate
PGA	phosphoglycerate
Pi	inorganic phosphate
PPi	inorganic pyrophosphate
TG	triglyceride
UMP, UDP, UTP	uridine 5'-mono-, -di-, -triphosphate

Common Enzymes

CPK	creatine phosphokinase
CS	citrate synthase
FBPase	fructose 1,6-bisphosphatase
α -GPDH	alphaglycerophosphate dehydrogenase

HK	hexokinase
IDH	isocitrate dehydrogenase
KGDH	α-ketoglutarate dehydrogenase
LDH	lactate dehydrogenase
MDH	malate dehydrogenase
ODH	octopine dehydrogenase
PDH	pyruvate dehydrogenase
PEPCK	phosphoenolpyruvate carboxykinase
PFK	phosphofructokinase
PGK	phosphoglycerate kinase
PK	pyruvate kinase

CONTENTS

List of Figures	vii
List of Tables	xiii
Preface	xv
List of Abbreviations	xix
CHAPTER ONE. Biochemical Adaptation: Basic Mechanisms and Strategies	3
CHAPTER TWO. Design of Cellular Metabolism	15
CHAPTER THREE. Adaptation of Enzymes to Metabolic Functions	55
CHAPTER FOUR. Exercise Adaptations	85
CHAPTER FIVE. Limiting Oxygen Availability	145
CHAPTER SIX. Metabolic Adaptations to Diving	182
CHAPTER SEVEN. Off-Switches in Metabolism: From Anhydrobiosis to Hibernation	204
CHAPTER EIGHT. Mammalian Developmental Adaptations	250
CHAPTER NINE. Respiratory Proteins	279
CHAPTER TEN. Water-Solute Adaptations: The Evolution and Regulation of Biological Solutions	304
CHAPTER ELEVEN. Temperature Adaptation	355
CHAPTER TWELVE. Adaptations to the Deep Sea	450
References	496
Index	522

FIGURES

2-1.	Summary block diagram of major functional units of cellular metabolism	17
2-2.	Major fermentation pathways in animal tissues	24
2-3.	The Krebs cycle as the hub of cellular metabolism	30
2-4.	Simplified diagram of the main sources of long-chain acylCoA for β -oxidation in mitochondria	31
2-5.	Diagrammatic summary of the urea cycle which is compartmentalized between cytosol and mitochondria	37
2-6.	Entry sites for the free amino acid pool into the Krebs cycle	40
2-7.	Electron transfer system showing three ATP conservation sites and entry sites for electrons and protons from various substrates	44
2-8.	Schematic diagram of the components of the electron-transfer chain and of the ATP-synthesizing components in a sul.mitochondrial particle	45
2-9.	Malate-aspartate shuttle as a mechanism for transferring reducing equivalents from cytosol to mitochondria	45
2-10.	The α -glycerophosphate hydrogen shuttle	46
2-11.	A schematic summary of the basic events of oxidative phosphorylation as they are currently interpreted by the chemi-osmotic theory	48
3-1.	Reaction rate plotted against substrate concentration for a reaction obeying Michaelis-Menten (or saturation) kinetics	59
3-2.	Rate of the reaction catalyzed by yeast phosphofructokinase as a function of the concentration of ATP in the absence of AMP	64
3-3.	The influence of the modulators phosphoenolpyruvate (PEP) and AMP on the regulatory kinetic behavior of <i>Mytilus</i> adductor PFK	67
3-4.	Upper panel: Velocity of the reaction catalyzed by a cooperative enzyme as a function of substrate concentration, showing effects of changes in $[S]_{0.5}$ Lower panel: Same as for upper panel except curves represent an enzyme showing Michaelis-Menten kinetics, where effects of change in $[S]$ or in K_m are much reduced	68
3-5.	Summary diagram of two key regulatory mechanisms in the PFK-FBPase catalyzed interconversion of F6P and F1,6BP	71
3-6.	Control cascade for activation of glycogen phosphorylase	76
4-1.	Regulatory properties of glycogen fermentation to lactate in vertebrate muscles	94
4-2.	Role of F2,6BP in the control of muscle phosphofructokinase	96

4-3.	Buffering capacities (β) in white skeletal muscle of different marine teleost fishes plotted against LDH activity of the muscles	100
4-4.	Enzyme cascade in the control of lipase catalyzed hydrolysis of tri-, di-, and monoglycerides	108
4-5.	Favored direction of aspartate aminotransferase function during Krebs cycle augmentation	111
4-6.	Roles of cytosolic CPK' and CPK _m in shuttling high energy phosphate from sites of ATP formation to sites of ATP utilization	114
4-7.	Graphic representation of hypothetical ADP saturation curves for muscle mitochondria from trained versus untrained individuals	118
4-8.	Scaling of LDH, PK, and CS activities in muscle (circles) and brain (squares) of <i>Paralabrax clathratus</i> and <i>P. nebulifer</i>	126
4-9.	Krebs cycle augmentation mechanism in bee flight muscle	130
4-10.	Possible use during recovery from strenuous anoxic work of glycogen \rightarrow strombine fermentation (as a source of ATP) and the ODH back-reaction (as a source of arginine) for recharging the arginine phosphate reserves	134
5-1.	Mutually exclusive processes of nitrate- and O ₂ -based respiration in denitrifiers	148
5-2.	Metabolic functions during O ₂ lack of Krebs cycle reactions in facultatively anaerobic bacteria and yeast	151
5-3.	The PEP branchpoint in bivalve molluscs and other facultatively anaerobic invertebrates	157
5-4.	Effect of pH on proton stoichiometry of ATP hydrolysis and of glycogen glucose fermentation	166
5-5.	Possible routes from pyruvate to ethanol in anoxic goldfish	171
6-1.	Upper panel: Tissue glycogen concentration changes (in μ moles glucosyl unit/gm wet weight of tissue) during twelve hours of submergence and recovery in the African lungfish Lower panel: Tissue and blood glucose concentration changes during twelve hours of submergence and recovery in the African lungfish	184
7-1.	Trehalose and glycogen contents of quick-dried <i>A. avenae</i> and of anhydrobiotic <i>A. avenae</i> in air and at intervals following transfer of the anhydrobiotic worms to water	214
7-2.	Levels of glycogen, polyols, and sugars in <i>Eurosta</i> larvae acclimated to subzero temperatures	217
7-3.	The Krebs cycle shown as a possible source of reducing power for sorbitol formation in <i>Eurosta</i> larval diapause	221
7-4.	Cross-sectional view of the tail region of the African lungfish, showing extensive depots of fat (dark staining regions)	224
7-5.	Metabolic map of probable metabolic fate of most of the amino	

acid pool in fish muscle during active mobilization of protein as an energy source	227
7-6. Apparent metabolic functions during bouts of arousal in small hibernators	232
7-7. Time course of blood urea changes following urea loading in the ground squirrel and in the laboratory rat	240
7-8. Metabolic organization during hibernation in bears	246
8-1. Diagrammatic representation of major mammalian developmental periods	251
8-2. Strategic role of the placenta illustrated through the metabolic and physiological roles of human placental lactogen (HPL)	253
8-3. Schematic representation of the methodology used in the study of uteroplacental metabolism, showing sampling sites for assay of metabolite levels and infusion sites for kinetic studies	254
8-4. Summary of net substrate fluxes in and through the ovine uteroplacenta in the last two weeks of gestation	254
8-5. Diagrammatic representation of changing LDH patterns during the development of the mouse kidney	257
8-6. Summary of metabolic events in liver of neonatal rats at suckling stage	269
8-7. Changes in nutrient composition of food consumed by fetal, suckling, weanling, and weaned rats, showing the relationship to changes in metabolic organization	274
8-8. Anapleurotic contribution of glucose to brain metabolism in the immature rat	278
9-1. Oxygen binding curves for different vertebrate hemoglobins (Hbs) as functions of Hb variant, modulator concentration, and temperature	282
9-2. The relationship between body size and degree of Bohr effect for Hbs from different mammals	291
9-3. The effects of pH on the P_{50} value of stripped (no ATP) and ATP-associated Hbs of the primitive salamander, <i>Amphiuma means</i>	292
9-4. Changes in blood parameters during acclimation of the killifish, <i>Fundulus heteroclitus</i> , to hypoxic conditions	294
9-5. Oxygen equilibrium curves of whole blood of <i>Fundulus heteroclitus</i> individuals possessing different lactate dehydrogenase (LDH) genotypes	295
9-6. The relationship between blood 2,3-diphosphoglycerate (2,3-DPG) concentration and oxygen binding ability (P_{50}) during postnatal development of the rat	297
10-1. The Hofmeister (lyotropic) series of neutral salts, arranged in order of their tendencies to stabilize or destabilize macromolecular structure	312

10-2.	A. The effects of different solutes on the maximal velocity (V_{\max}) of the <i>Pachygrapsus crassipes</i> pyruvate kinase reaction. B. The effects of different solutes on the apparent Michaelis constant (K_m) of phosphoenolpyruvate (PEP) of the <i>P. crassipes</i> pyruvate kinase reaction	314
10-3.	The effects of different solutes on the apparent Michaelis constant (K_m) of NADH of tuna M_4 -lactate dehydrogenase	315
10-4.	The effects of salt and glycerol on the activity of glucose-6-phosphate dehydrogenase from <i>Dunaliella tertiolecta</i> and <i>D. viridis</i>	315
10-5.	The counteracting influences of urea and methylamine solutes (TMAO, betaine, sarcosine) on the kinetic characteristics of different enzymic reactions	323
10-6.	The effects of different solutes on the thermal transition temperature of bovine pancreatic ribonuclease	325
10-7.	The requirements of elasmobranch M_4 -lactate dehydrogenases for physiological concentrations of urea	327
10-8.	The effects of Hofmeister series salts (plus n-propanol) on the V_{\max} of the malate dehydrogenase (MDH) reaction of the extreme halophilic bacterium, <i>Halobacterium halobium</i>	335
10-9.	The imidazole group of histidine showing protonated and non-protonated states	337
10-10.	The active center of lactate dehydrogenase, showing the key residues involved in pyruvate binding	339
10-11.	The influences of pH on the kinetic and structural properties of phosphofructokinase (PFK)	343
10-12.	"The importance of being ionized": the influence of pH on the ionization state of key biomolecules	347
10-13.	Three forms of a given type of enzyme, all of which have the same catalytic capacity but which differ in apparent K_m of substrate	351
10-14.	Energy profiles for uncatalyzed and enzyme-catalyzed reaction sequences	352
11-1.	Energy distribution curves for a population of molecules at two different temperatures	357
11-2.	Brown adipose tissue mitochondrial function	366
11-3.	The PFK-FBPase futile cycle found in the thoracic muscle of bumblebees	369
11-4.	The circulatory pattern in a countercurrent heat exchanger	373
11-5.	Temperature compensation of oxygen consumption rates in fishes from different thermal regimens	377
11-6.	Free energy profiles for three versions of the same chemical reaction	379
11-7.	Compensation plots (ΔH^\ddagger versus ΔS^\ddagger) for the activation enthalpies and entropies of reactions catalyzed by interspecific homologues of different enzymes	384

11-8.	Energy profiles for the reactions catalyzed by two forms of an enzyme which differ in the energy changes that occur during binding and the activation event	387
11-9.	Substrate saturation curves for three variants of a given type of enzyme having different apparent K_m values	389
11-10.	Apparent K_m of pyruvate versus temperature for M_4 -LDHs of vertebrates having different adaptation temperatures	391
11-11.	The relationships of blood, muscle cytosol, and mitochondrial matrix pH to body temperature in animals	393
11-12.	The effect of experimental temperature on the apparent K_m of pyruvate of M_4 -LDHs of three vertebrates adapted to different temperatures	395
11-13.	Distribution patterns and electrophoretic and kinetic properties of M_4 -LDHs of four species of eastern Pacific barracudas	398
11-14.	The effects of temperature-dependent changes in K_m and [substrate] on the temperature coefficients (Q_{10}) of enzymic reactions	401
11-15.	The effect of temperature on the apparent Michaelis constant (K_m) of acetylcholine (ACh) for acetylcholinesterases from fishes adapted or acclimated (rainbow trout) to different temperatures	402
11-16.	Cytochrome oxidase activity in goldfish skeletal muscle as a function of time at different acclimation temperatures	407
11-17.	The time course of change in light-saturated photosynthetic capacity and fructose-1,6-bisphosphatase (FBPase) activity in mature leaves of <i>Nerium oleander</i> grown under different acclimation regimens	408
11-18.	The effects of temperature, pH, and [urea] on the catalytic stability and subunit assembly state of muscle phosphofructokinase purified from the ground squirrel, <i>Citellus beecheyi</i>	418
11-19.	Polymerization thermodynamic parameters and heat denaturation for skeletal muscle actins purified from animals having widely different body temperatures	421
11-20.	Some commonly occurring lipids in biological membranes	425
11-21.	The fluid-mosaic model of a biological membrane	425
11-22.	Fluidity-dependent regulation of desaturase activity in the endoplasmic reticulum membranes of <i>Tetrahymena</i>	429
11-23.	Time courses for acclimation for three behavioral traits and for synaptosome lipid fluidity in goldfish	430
11-24.	The effects of growth and assay temperatures on photosynthetic rates and chlorophyll fluorescence in a variety of plants adapted to different habitat temperatures	432
11-25.	Arrhenius plots for an ion-dependent ATPase from membranes of warm- and cold-adapted (-acclimated) organisms	434
11-26.	The effects of temperature on: 1) evaporative water loss in <i>Phyllomedusa sauvagei</i> and 2) evaporative water loss from the	

	surface of water covered with a film of lipid from skin secretions of this frog	435
11-27.	Structures of the glycopeptide and peptide antifreezes of polar fishes	443
12-1	Classification of the marine environments	451
12-2.	Sources of volume changes during enzymic reactions and protein subunit aggregation events	456
12-3.	The effects of hydrostatic pressure on the apparent K_m of NADH and pyruvate for purified M_4 -lactate dehydrogenases	459
12-4.	Depth distributions of several marine teleost fishes	460
12-5.	A compensation plot of the enthalpy and entropy changes accompanying the polymerization of muscle actin in several species of teleost fishes	469
12-6.	The effects of measurement pressure and temperature on the activity of the Na-K-ATPase of pig kidney	473
12-7.	The relationship between routine respiration, maximal respiration, and minimal depth of occurrence for a number of mid-water fishes	475
12-8.	The relationships between minimal depth of occurrence and lactate dehydrogenase-[LDH] and pyruvate kinase-[PK] activities of fish white skeletal muscle	478
12-9.	The relationship between routine oxygen consumption rates of midwater fishes and their skeletal muscle lactate dehydrogenase (LDH) and malate dehydrogenase (MDH) activities	482
12-10.	The hydrothermal vent communities	487
12-11.	<i>Riftia pachyptila</i> , a vestimentiferan tube worm found at the deep-sea hydrothermal vents.	490

TABLES

2-1. Energy Yields of Common Fuels for Metabolism	51
3-1. Error Rates and Editing	80
4-1. Relative Oxygen Consumption of Different Organs in Man as a Function of Work Rate	86
4-2. Estimated Maximum Power Output for Skeletal Muscle (of Man) Utilizing Different Substrates and Metabolic Pathways	87
4-3. Summary of Various Ultrastructural and Metabolic Features of Different Muscle Fiber types in Vertebrates	88
4-4. Cellular Energy Stores in Human Muscle	90
4-5. Preferred Energy Stores in Salmon and Squid	90
4-6. Adaptation of Levels of Citrate Synthase and LDH in White (WM) and Red Muscle (RM) in Selected Fishes	92
5-1. Glycogen Levels in Liver of Several Vertebrates Varying in Anoxia Tolerance	153
5-2. Phosphorylation Coupled to the Formation of Succinate	158
5-3. Proton Stoichiometry of Anaerobic Glycolysis and Glycogen \rightarrow Lactate Fermentation	163
5-4. H^+ Stoichiometry for Succinate Fermentation	164
5-5. H^+ Stoichiometry for Propionate Fermentation	164
5-6. H^+ Stoichiometry for ATP Hydrolysis	165
5-7. Fermentations Coupled to ATPases	167
6-1. Size and Metabolism of the Brain in the Weddell Seal during Experimental Diving Compared to Man at Rest	189
6-2. Brain Utilization of Blood Glucose in the Weddell Seal during Experimental Diving Compared to Man at Rest	190
6-3. Lung Metabolic Rate in the Weddell Seal during Experimental Diving Compared to Man at Rest	191
6-4. Metabolic Rates of Weddell Seal Heart at Varying Work Loads	192
6-5. Maximum Aerobic Diving Times in 450 kg Weddell Seal	194
6-6. Partitioning (Aerobic versus Anaerobic) Functions of Diving Response	195
7-1. Hydration-dependence of Cellular Metabolism in <i>Artemia</i> Cysts	208
7-2. Changes in Sugar, Polyol, and Glycogen Levels with Acclimation to Low Temperature in Comparison to Metabolite Concentrations in Larvae at 15°C	219
8-1. Enzyme Activities in the Liver of Fetal, Suckling, and Weaned Rats	275
9-1. The Major Structural and Functional Characteristics of the Oxygen Transport Proteins	280

9-2.	Properties of "Typical" and "Backup" Hemoglobins, including Trout Hb-I and Trout Hb-IV	286
9-3.	Functional Properties of Fry and Adult Hemoglobins of the Coho Salmon (<i>Oncorhynchus kisutch</i>)	290
10-1.	Intracellular Osmolyte Concentrations of Diverse Organisms, Illustrating the Major Classes of Solute Accumulation Patterns	306
10-2.	Free Amino Acid Contents in Body Fluids of Selected Marine Invertebrates	316
10-3.	A Comparison of Acidic and Basic Amino Acids and the Hydrophobicity of Cytoplasmic Soluble Proteins and Ribosomal Proteins from Halophilic and Nonhalophilic Bacteria	332
10-4.	Properties of Histidine Imidazole Groups	338
10-5.	Structure, Properties, and Sites of Occurrence of Dipeptide Buffers	345
11-1.	The Approximate Enthalpy Changes Associated with the Formation of Weak Bonds	358
11-2.	Biological Structures and Processes which are Dependent on Weak Chemical Bonds for Their Precision and Efficiency	359
11-3.	Enthalpy Balances during Substrate Oxidations	364
11-4.	Activation Parameters for Sets of Homologous Enzymic Reactions of Species Differing in Adaptation Temperature	381
11-5.	Pyruvate Concentrations in Skeletal Muscle of Different Vertebrates	391
11-6.	Kinetic Parameters for the Lactate Dehydrogenase Reactions of Three Barracuda Congeners	399
11-7.	The Effects of Substrate Concentrations on Q_{10} Values for Enzymic Reactions in which the K_m of Substrate Increases with Rising Temperature	400
11-8.	Thermal Stabilities of Homologous Proteins from Organisms Adapted to Different Temperatures	410
11-9.	Structures and Melting Temperatures for Commonly Occurring Fatty Acids	426
11-10.	Fatty Acid Composition of Phosphoglycerides from Brain Synaptosomes Isolated from Animals Acclimated to or Adapted to Different Temperatures	427
11-11.	"Antifreeze" Proteins and Glycoproteins of Fishes and Invertebrates	440
12-1.	Activation Energy Parameters and Relative Absolute Velocities of M_4 -Lactate Dehydrogenase Reactions of Species Adapted to Different Temperatures and Pressures	463
12-2.	Enzymic Activities of White Skeletal Muscle and Brain and Muscle Water Content, Protein Concentration, and Buffering Capacity of Marine Fishes Having Different Depths of Distribution and Feeding and Locomotory Habits	480
12-3.	Comparisons of Muscle and Brain Biochemistries of <i>Sebastes alascanus</i> and <i>S. altivelis</i>	484