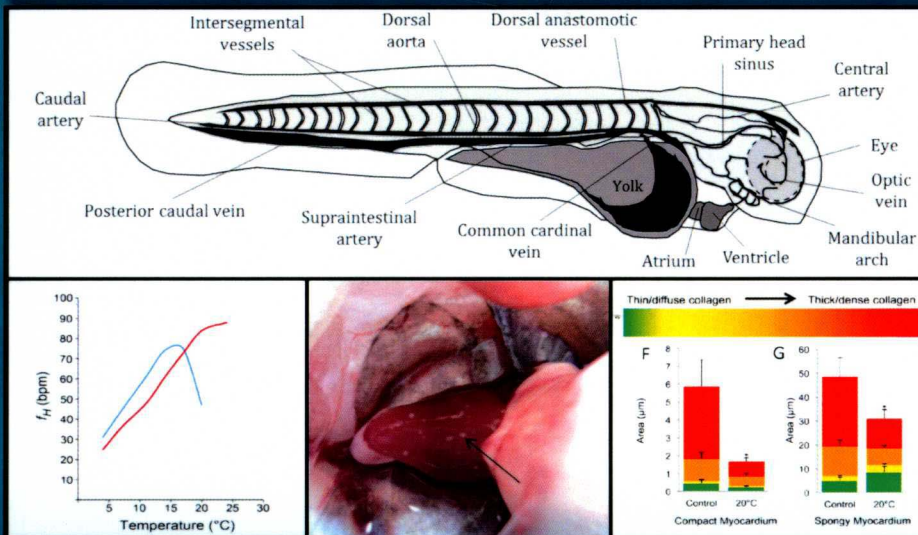


# The Cardiovascular System

Development, Plasticity  
and Physiological Responses



A. Kurt Gamperl, Todd E. Gillis,  
Anthony P. Farrell, and Colin J. Brauner

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# THE CARDIOVASCULAR SYSTEM: DEVELOPMENT, PLASTICITY AND PHYSIOLOGICAL RESPONSES

Fish Physiology

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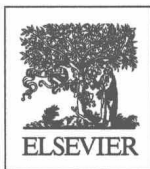
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## ABBREVIATIONS

- 2,3-DPG** 2,3-diphosphoglycerate  
**4-HT** 4-hydroxytamoxifen  
**5-HD** sodium 5-hydroxydecanoic acid  
**5-HT** 5-hydroxytryptamine (serotonin)  
**A** atrium  
**AA** arachidonic acid  
**A<sub>o</sub>** ventral aorta  
**ABA** afferent branchial arteries  
**ACE** angiotensin-converting enzyme  
**ACH** acetylcholine  
**ACV** anterior cardinal vein  
**AD** adrenaline  
**ADO** adenosine  
**ADP** adenosine diphosphate  
**ADP<sub>50</sub>** ratio of atrial to ventricular action potential duration  
**AE** anion exchange or  $\text{Cl}^-/\text{HCO}_3^-$  exchanger  
**AFA** afferent filamental arteries  
**AGD** amoebic gill disease  
**AIP** AHR-interacting protein  
**AKAP** A-kinase anchoring protein  
**AHR** aryl hydrocarbon receptor  
**ALAs** afferent lamellar arterioles  
**AMP** adenosine monophosphate  
**AMPA** alpha-amino-3-hydroxy-5-methylisoxazole-4-propionic acid  
**AMPK** AMP-activated protein kinase  
**AMs** adrenomedullins  
**ANG-1** angiopoietin 1  
**AngII** angiotensin II  
**ANP** atrial natriuretic peptide  
**ANRT** AHR nuclear receptor translocator

- AOP** adverse outcome pathway  
**APC** antigen-presenting cells  
**AP** action potential  
**AR** adrenoreceptor  
**ARC** activity-regulated cytoskeleton-associated protein  
**ASCV** Atlantic salmon calcivirus  
**ASN** anterior spinal nerve  
**ASR** aquatic surface respiration  
**AT<sub>1</sub>** angiotensin 1 receptor  
**AT<sub>2</sub>** angiotensin 2 receptor  
**ATP** adenosine triphosphate  
**A.U.** arbitrary units  
**A-VO<sub>2</sub>** difference between the oxygen content of arterial and venous blood,  
also known as tissue oxygen extraction  
**AV** atrioventricular  
**AVP** atrioventricular plexus  
**AVR** atrioventricular region  
**AVT** arginine vasotocin  
**Ax** axillary body  
**AZ** acetazolamide  
**α-AR** alpha adrenoreceptor  
**β<sub>2</sub>-AR** β<sub>2</sub>-type adrenoreceptor  
**BA** bulbus arteriosus  
**β<sub>b</sub>** capacitance of blood for O<sub>2</sub>  
**BCR** branchial cardiac ramus  
**BCT** branchiocardiac nerve trunk  
**BKs** bradykinins  
**BLs<sup>-1</sup>** swimming speed expressed as body lengths per second  
**B<sub>max</sub>** receptor density  
**BMP** bone morphogenic protein  
**BN** branchial nerve  
**β-NHE** β-adrenergic Na<sup>+</sup>-H<sup>+</sup> exchanger  
**BNP** brain natriuretic peptide  
**bpm** beats per minute  
**BV** branchial vein  
**BZ** benzolamide  
**C** conus or compliance  
**CA** carbonic anhydrase  
**Ca<sup>2+</sup>** calcium  
**[Ca<sup>2+</sup>]<sub>i</sub>** intracellular free Ca<sup>2+</sup> concentration  
**CAM** chorioallantoic membranes  
**cAMP** cyclic adenosine monophosphate  
**CaN** calcineurin

- C<sub>a</sub>O<sub>2</sub>** arterial O<sub>2</sub> content  
**CASQ2** calsequestrin 2  
**CAT** catecholamines  
**CaTF** Ca<sup>2+</sup> sensitive transcription factors  
**CBF** coronary blood flow  
**CBS** cystathionine beta-synthase  
**CCO** cytochrome *c* oxidase  
**CCK** cholecystokinin  
**CD73** ecto-5'-nucleotidase  
**CdA** caudal artery  
**CDβ** β COMMA-D cell line engineered to express β-galactosidase  
**CdV** caudal vein  
**CgA** chromogranin A  
**cGMP** cyclic guanosine monophosphate  
**CGRP** calcitonin gene-related peptide  
**ChAT** choline acetyltransferase  
**CICR** Ca<sup>2+</sup>-induced Ca<sup>2+</sup>-release  
**CK** creatine kinase  
**cKit** receptor tyrosine kinase  
**cmIc** myosin light chain polypeptide  
**CMA** coeliacomesenteric artery  
**CMS** cardiomyopathy syndrome  
**cNOS** constitutive nitric oxide synthase  
**CNP** C-type natriuretic peptide  
**CNS** central nervous system  
**CO** carbon monoxide  
**CO<sub>2</sub>** carbon dioxide  
**C<sub>O<sub>2</sub></sub>** content of O<sub>2</sub> in blood  
**CoA** coenzyme A  
**COL1A1** collagen Type I alpha 1 chain gene  
**COX** cyclooxygenase  
**CP** creatine phosphate  
**CPCs** cardiac progenitor cells  
**CPO** cardiac power output  
**CPO<sub>max</sub>** maximum cardiac power output  
**CPO<sub>sys</sub>** systemic cardiac power output  
**CPT** carnitine palmitoyltransferase  
**Cr** creatine  
**CR** crural cardiac ramus  
**CrA** carotid arteries  
**CS** citrate synthase  
**C<sub>s</sub>** the slope of the capacitance curve  
**CSE** cystathionine gamma-lyase



- CSPN** cardiac spinal pre-ganglionic neuron  
**CSQ** calsequestrin  
**CSQ2** cardiac isoform of calsequestrin  
**CST** catestatin  
**CTGF** connective tissue growth factor  
 **$CT_{\max}$**  critical thermal maximum  
**cTnC** cardiac troponin C  
**cTnI** cardiac troponin I  
**cTnT** cardiac troponin T  
**CV** conal valves  
 **$C_vO_2$**  venous  $O_2$  content  
**CVS** central venous sinus  
**CVPN** cardiac vagal pre-ganglionic neuron  
**CYP1A** cytochrome P450 1A  
**CYS** cysteine  
**d** day  
**DA** dorsal aorta  
**DC** ductus of Cuvier  
**DDT** dichlorodiphenyltrichloroethane  
**DIDS** 4,4'-diisothiocyano-2,2'-stilbenedisulfonic acid  
**DLCs** dioxin-like compounds  
**DMO** 5,5-dimethyl-2,4-oxazolidinedione  
**DNA** deoxyribonucleic acid  
**DPI** days post-injury  
**DPF** days post-fertilization  
**DPT** days post-treatment  
**dsRNA** double-stranded RNA  
 **$\Delta G_{ATP}$**  Gibbs free energy per mole of hydrolyzed ATP  
 **$\Delta P$**  change in pressure (pressure difference)  
 **$\Delta pH_{a-v}$**  arterial–venous pH difference  
 **$\Delta P_v$**  pressure gradient that drives venous return  
 **$\Delta S_{a-v}O_2$**  change in arterial–venous Hb– $O_2$  saturation (see below)  
 **$\Delta V$**  change in volume  
 **$E_{a-v}O_2$**  extraction of  $O_2$  at the tissues  
**EBA** efferent branchial arteries  
**E–C** excitation–contraction  
**ECG** electrocardiogram  
**ECM** extracellular matrix  
**ECs** endocardial cushions  
**EDCF** endothelium-derived contracting factors  
**EDRF** endothelium-derived relaxing factors  
**EE** endocardial endothelium  
**EFAs** efferent filamental arteries

- EGCs** eosinophilic granular cells  
 **$E_{ion}$**  equilibrium potential  
**EIPA** ethyl isopropyl amiloride  
 **$E_{K^+}$**  equilibrium potential for  $K^+$   
**ELAs** efferent lamellar arterioles  
**EM** electron microscopy  
 **$E_m$**  membrane potential  
**EMT** epithelial-to-mesenchymal transition  
 **$E_{Na^+}$**  equilibrium potential for  $Na^+$   
**eNOS** endothelial nitric oxide synthase  
**EPA** eicosapentanoic acid  
**EPDCs** epicardial-derived cells  
**EPO** erythropoietin  
**EPOR** EPO receptor  
**ERG** erythroblast transformation-specific -related gene  
**ERG channel** ether-à-go-go-related gene  $K^+$  channel  
**ERK** extracellular signal-regulated kinase  
**ET** endothelins  
**E-T** excitation-transcription  
**ET-1** endothelin-1  
**ETA** eicosatetranoic acid  
 **$F$**  Faraday's constant  
 **$F_C$**  flow rate through chamber  
**FGF** fibroblast growth factor  
 **$f_H$**  frequency of the heartbeat, or heart rate  
 **$f_{Hmax}$**  maximum cardiac frequency or maximum heart rate  
**FP** flow probe  
**FKBP12** 12-kDa FK506-binding protein  
 **$f_R$**  respiratory frequency  
**Fs** Furans  
**G6P** glucose-6-phosphate  
 **$G\alpha13$**  G protein subunit  $G\alpha13$   
**GA** gill arch  
**GBF** gonad blood flow  
**GC** guanylate cyclase  
**GF** gill filaments  
 **$G_i$**  inhibitory G protein  
 **$G_o$**  gonad  
**GLUTs** glucose transporter proteins  
**GPCR** G protein-coupled receptor  
**GPI** glycosphosphatidylinositol  
 **$G_s$**  stimulatory G protein  
**GTP** guanosine triphosphate

- G<sub>u</sub>** gut  
**H** heart  
**h** hour  
**H<sup>+</sup>** hydrogen ion  
**Hb** hemoglobin  
**[Hb]** hemoglobin concentration  
**Hct** hematocrit  
**HCN channel** family of hyperpolarization-activated, cyclic nucleotide-gated, ion channels involved in controlling the pacemaker  
**HEK cells** human embryonic kidney cells  
**HEP** high energy phosphate  
**HH** hedgehog  
**HIF-1** hypoxia inducible factor 1  
**HIF 1- $\alpha$**  hypoxia inducible factor 1- $\alpha$   
**HK** hexokinase  
**HO** heme oxygenase.  
**HOAD**  $\beta$ -hydroxyacyl CoA dehydrogenase  
**hpf** hours post-fertilization  
**HPV** hepatic portal vein  
**HSMI** heart and skeletal muscle inflammation  
**HSP** heat shock proteins  
**H<sub>2</sub>S** hydrogen sulfide  
**HV** hepatic vein  
**I<sub>Ca</sub>** Ca<sup>2+</sup> current  
**I<sub>CaL</sub>** L-type Ca<sup>2+</sup> current  
**I<sub>CaT</sub>** T-type Ca<sup>2+</sup> current  
**ICN** intracardiac neuron  
**ICNS** intracardiac nervous system  
**I<sub>f</sub>** pacemaker current, “funny” current  
**IFN $\alpha$**  interferon alpha  
**IFN $\gamma$**  interferon gamma  
**IGF-1** insulin-like growth factor 1  
**IgM** immunoglobulin  
**I<sub>KACH</sub>** acetylcholine-activated inward rectifier current  
**I<sub>KATP</sub>** ATP-sensitive inward rectifier current  
**I<sub>K1</sub>** inward-rectifier K<sup>+</sup> current  
**I<sub>Kr</sub>** delayed-rectifier K<sup>+</sup> current  
**I<sub>Na</sub>** Na<sup>+</sup> current  
**I<sub>NCX</sub>** Na<sup>+</sup>-Ca<sup>2+</sup> exchange current  
**iNOS** inducible NO synthase  
**ION<sub>f</sub>** intracellular “free” ion concentration  
**ION<sub>e</sub>** extracellular “free” ion concentration  
**IP<sub>2</sub>** inositol diphosphate

- IP<sub>5</sub>** inositol pentaphosphate  
**IRK2** inwardly rectifying K<sup>+</sup> channel 2  
**I/R** ischemia–reperfusion  
**ISA** infectious salmon anemia  
**ISG15** interferon-stimulated gene 15  
**ISL1** transcription factor islet 1  
**ISO** isoproterenol  
**JAK1** janus kinase 1  
**JNK** C-jun NH<sub>2</sub> terminal kinase  
**JV** jugular vein  
**K<sub>ATP</sub>** ATP-sensitive K<sup>+</sup> channels  
**K<sub>Ca</sub>** Ca<sup>2+</sup>-activated K<sup>+</sup> channels  
**K<sub>cat</sub>** turnover number  
**K<sub>d</sub>** receptor binding affinity  
**kDa** kilo Dalton  
**K<sub>eq</sub>** equilibrium constant  
**K<sup>+</sup>** potassium ion  
**K<sup>+</sup>/Cl<sup>-</sup>** potassium chloride co-transport  
**[K<sup>+</sup>]<sub>e</sub>** extracellular K<sup>+</sup> concentration  
**[K<sup>+</sup>]<sub>i</sub>** intracellular K<sup>+</sup> concentration  
**K<sub>H</sub>** hydration rate constant  
**KH7** blocker of soluble guanylate cyclase  
**k<sub>i</sub>** inhibition constant  
**K<sub>ir</sub>** inward rectifier K<sup>+</sup> channels  
**L** vessel length  
**La** lamella  
**L-AA** L-ascorbic acid  
**L-ARG** L-arginine  
**LCV** lateral cutaneous vein  
**LDA** length-dependent activation  
**LDH** lactate dehydrogenase  
**L-NMMA** L-N<sup>G</sup>-monomethyl-L-arginine  
**LTCC** L-type Ca<sup>2+</sup> channels  
**M<sub>2</sub>R** muscarinic type-2 receptor  
**MAPK** mitogen-activated protein kinase  
**max dP/dt<sub>sys</sub>** maximal rate of pressure change during systole  
**max dP/dt<sub>dia</sub>** minimum rate of pressure change during diastole  
**M<sub>b</sub>** body mass  
**MCFP** mean circulatory filling pressure  
**MCT** monocarboxylate transporters  
**MD** medulla  
**MHC** major histocompatibility complex  
**min** minute

- miRNAs** microRNAs  
**miR-133** microRNA 133  
**MLP** muscle LIM protein  
**MMPs** matrix metalloproteinases  
 **$\dot{M}O_2$**  rate of oxygen consumption  
 **$\dot{M}O_{2max}$**  maximum rate of oxygen consumption  
**MPP5** membrane palmitoylated protein 5  
**mRNA** messenger RNA  
**ms** milliseconds  
 **$M_V$**  mass of ventricle  
**MY** million years  
 **$Na^+$**  sodium  
**NAD** noradrenaline  
**NANC** non-adrenergic non-cholinergic  
**NCX**  $Na^+/Ca^{2+}$ -exchanger  
**NECs** neuroepithelial cells  
**NeKA** neurokinin A  
**NF- $\kappa$ B** nuclear factor kappa light chain enhancer of activated B cells  
 **$\eta_H$**  hill coefficient  
**NHE**  $Na^+-H^+$  exchanger  
**NKA**  $Na^+-K^+$ -ATPase  
**NMDA** *N*-methyl-D-aspartate  
**NPs** natriuretic peptides (ANP, BNP, CNP, VNP)  
**NPR** natriuretic peptide receptor (A, B, C, D, V)  
**NO** nitric oxide  
 **$NO_2^-$**  nitrite  
**NOAA** National Oceanic and Atmospheric Association  
**NOK** novel oncogene with kinase domain  
**NOS** nitric oxide synthase  
**NPY** neuropeptide Y  
**NTP** nucleotide triphosphate  
**O** ostium of sinoatrial valve  
 **$O_2$**  oxygen  
**OEC**  $O_2$  equilibrium curve  
**OFT** outflow tract  
***P*** atrioventricular plug  
 **$P_{50}$**  partial pressure of  $O_2$  at which 50% of hemoglobin is bound to oxygen  
 **$P_A$**  arterial blood pressure  
 **$Pa_{50}$**  arterial  $P_{50}$   
**PACs** polycyclic aromatic compounds  
**PACA** plasma-accessible carbonic anhydrase  
 **$P_aCO_2$**  arterial partial pressure of carbon dioxide

- PAF1** polymerase-associated factor 1  
**PAHs** polycyclic aromatic hydrocarbons  
**PAK** p21-activated kinase  
 **$P_aO_2$**  arterial partial pressure of  $O_2$   
**pCa** calcium concentration, expressed as  $-\log$   
**pCa<sub>50</sub>**  $P_{Ca}$  for half maximal activation  
**PCBs** polychlorinated biphenyls  
**PCDD** polychlorinated dibenzo-*p*-dioxins  
**PCNA** proliferating cell nuclear antigen  
**PCO<sub>2</sub>** partial pressure of  $CO_2$   
**PCR** polymerase chain reaction  
**PCS** posterior cardinal sinus  
**PCV** posterior cardinal veins  
 **$P_{CV}$**  central venous blood pressure  
**PD** pancreas disease  
 **$P_{DA}$**  dorsal aortic pressure  
**PDH** pyruvate dehydrogenase  
**PE** phenylephrine  
**PFK** 6-phosphofructokinase  
**PGE2** prostaglandin E2  
**pH<sub>a</sub>** arterial pH  
**pH<sub>e</sub>** extracellular pH  
**pH<sub>i</sub>** intracellular pH  
**PHZ** phenylhydrazine  
 **$P_i$**  inorganic phosphate  
**PICA** plasma inhibitors of carbonic anhydrase  
**PI-PLC** phosphatidylinositol specific phospholipase C  
 **$P_{in}$**  input pressure  
**PK** pyruvate kinase  
**PKC** protein kinase C  
**PKG** protein kinase G  
**PLB** phospholamban  
**PMCA** plasma membrane  $Ca^{2+}$ -ATPase  
**PMCV** piscine myocarditis virus  
**PO<sub>2</sub>** partial pressure of  $O_2$   
 **$P_{out}$**  output pressure  
**proANF** atrial natriuretic factor prohormone  
**PRV** piscine reovirus  
**PTx** pertussis toxin  
**PUFA** polyunsaturated fatty acids  
**PV** pulmonary vein  
 **$P_V$**  plasma volume

- $P_{\text{ven}}$  venous pressure  
 $P_{\text{v}50}$  venous  $P_{50}$   
 $P_{\text{vO}_2}$  venous partial pressure of oxygen  
 $P_{\text{vA}}$  blood pressure in the ventral aorta  
 $\dot{Q}$  cardiac output  
 $\dot{Q}_{\text{max}}$  maximum cardiac output  
 $Q_{10}$  temperature quotient; the ratio of a rate function over a 10°C temperature difference  
qPCR quantitative polymerase chain reaction  
 $r$  vessel radius  
 $R$  vascular resistance  
RA retinoic acid  
RAS renin–angiotensin system  
RBC red blood cell  
 $R_{\text{cor}}$  vascular resistance of the coronary circulation  
RD2 retinaldehyde dehydrogenase 2  
ReA renal artery  
 $R_{\text{gill}}$  vascular resistance of the gill circulation  
RMP resting membrane potential  
RNA-Seq high-throughput RNA sequencing  
ROS reactive oxygen species  
RQ respiratory quotient  
 $R_{\text{sys}}$  vascular resistance of the systemic circulation  
rTNF- $\alpha$  recombinant tumor necrosis factor- $\alpha$   
 $R_{\text{tot}}$  total peripheral vascular resistance  
RyR ryanodine receptor  
 $R_v$  resistance to venous return  
RVM relative ventricular mass (mass of the ventricle relative to body mass, expressed as a percentage)  
RVR resistance to venous return  
S1P lysosphingolipid sphingosin-1-phosphate  
S1Pr2 lysosphingolipid sphingosin-1-phosphate receptor 2  
SA sinoatrial  
sAC soluble adenylyl cyclase  
SA node sinoatrial node  
SAP sinoatrial plexus  
SAR sinoatrial region  
SAV salmonid alphavirus  
 $S_{\text{a-vO}_2}$  difference in arterial–venous Hb–O<sub>2</sub> saturation  
SBV stressed blood volume  
SC spinal cord  
SCA subclavian artery

- SCP** salmon cardiac peptide  
**SCV** subclavian vein  
**SD** sleeping disease  
**SDS** sodium dodecyl sulfate  
**SEM** scanning electron microscope  
**SERCA** sarco-endoplasmic reticulum  $\text{Ca}^{2+}$ -ATPase  
**SeV** subepithelial vein  
**SG** sympathetic ganglia  
**SGC** soluble guanylate cyclase  
**SIV** suprainestinal vein  
**SL** sarcolemma or sarcolemmal  
 **$SL_n$**  sarcomere length  
**SMLC2** slow myosin light chain 2  
**SN** spinal nerve  
**SNP** sodium nitroprusside  
**SNS** sympathetic nervous system  
**SPN** spinal pre-ganglionic neurons  
 **$\text{SO}_2$**  Hb- $\text{O}_2$  saturation (arterial  $\text{S}_a\text{O}_2$  and venous  $\text{S}_v\text{O}_2$ )  
**SP** substance P  
**SR** sarcoplasmic reticulum  
**SUR** sulfonyleurea receptor  
**SV** sinus venosus  
 **$t_{1/2}$**  half-time  
**TBX** T-box transcription factor  
**TCA cycle** tricarboxylic acid cycle  
**TCDD** 2,3,7,8-tetrachlorodibenzo-*p*-dioxin  
**TCR** T-cell receptor  
**TDEE** temperature-dependent deterioration of electrical excitation  
**TdT** dUTP nick-end labeling  
**TEFs** toxicity equivalence factors  
**TGF- $\beta_1$**  transforming growth factor-beta 1  
**TIMP** tissue inhibitor of metalloproteinase  
**TM** tropomyosin  
**TMAC** transmembrane adenylyl cyclase  
**TnC** troponin C  
**TnI** troponin I  
**TNF- $\alpha$**  tumor necrosis factor-alpha  
 **$\text{TO}_{2\text{max}}$**  maximum arterial  $\text{O}_2$  transport  
 **$T_{\text{optAS}}$**  optimal temperature for aerobic scope  
**TUNEL** terminal deoxynucleotidyl transferase  
**UI** urotensin I  
**UII** urotensin II



- $U_{\text{crit}}$  critical swimming speed of a fish  
**UDP** uridine diphosphate  
**UK** United Kingdom  
**Us** urotensins  
**USBV** unstressed blood volume  
**UTP** uridine triphosphate  
**UTR** 3'-untranslated region  
 $V$  ventricle  
 $V_{\text{b}}$  blood volume  
 $\dot{V}_{\text{b}}$  blood flow  
**VC** vena cava  
**VCR** visceral cardiac ramus of vegas  
**VEGF** vascular endothelial growth factor  
**VIP** vasoactive intestinal peptide  
 $V_{\text{m}}$  resting membrane potential  
**VMHC** ventricular myosin heavy chain  
**VNP** ventricular natriuretic peptide  
**VO** vascular occluder  
 $\dot{V}\text{O}_2$   $\text{O}_2$  uptake per unit time  
 $V_{\text{R}}$  total ventilation volume  
**VS** vasostatin  
 $V_{\text{s}}$  stroke volume, volume of blood pumped with each heartbeat  
 $V_{\text{smax}}$  maximum stroke volume  
**VS-1** vasostatin 1  
**VS-2** vasostatin 2  
**VST** vagosympathetic trunk  
**WAF** water accommodated fraction  
 $W_{\text{S}}$  stroke work  
**WT1** Wilms' tumor protein 1  
 $X$  cardiac vagus rami  
**X1** lateral vagal motor neuron group  
 $X_{\text{br}}$  vagal ramus interconnecting gill arches  
 $X_{\text{m}}$  medial vagal motor neuron group  
 $X_{\text{mr}}$  rostral components of the medial vagal motor neuron group  
 $X_{\text{mc}}$  caudal components of the medial vagal motor neuron group  
 $X_{\text{r}}$  vagal root  
 $\Phi$  Bohr-coefficient  
 $\eta$  fluid viscosity