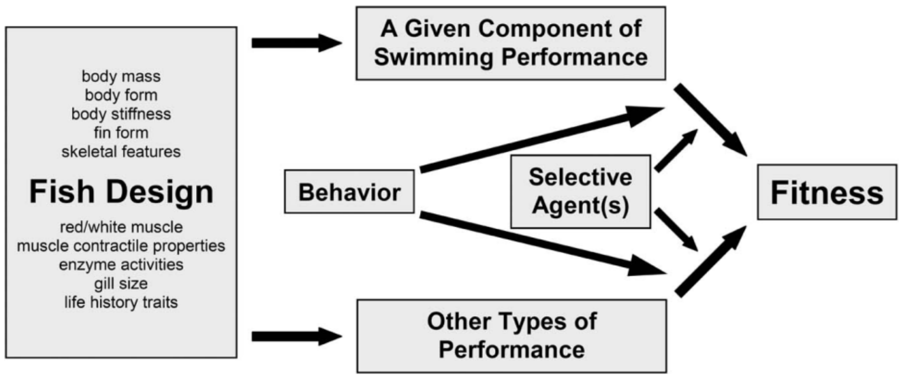
Exercise in Fish

- Greater response than in mammals
- Longer time to correct or recover
- Diverse evolutionary pathway
- Poikilotherms likely different
- Most fish have much larger relative muscle mass than terrestrial homeotherms - why is that?

Locomotion and Swimming

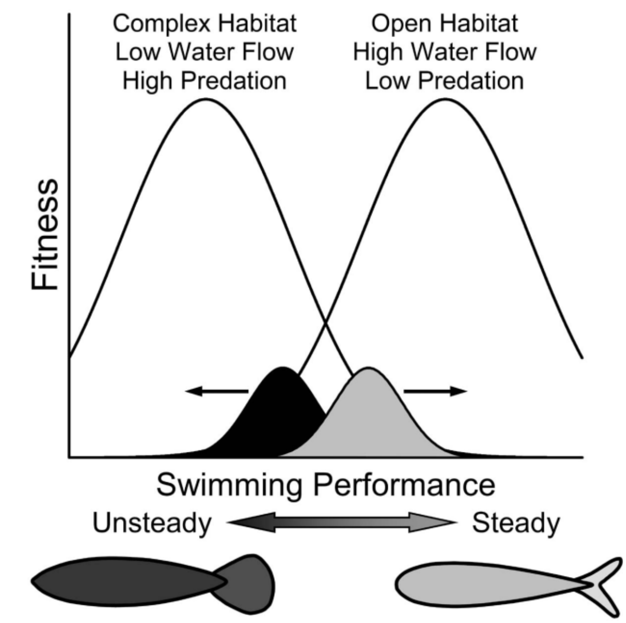
- Different categories
  - Rest
  - Swimming at constant velocity
  - Swim to accelerate



Langerhans, R.B., and Reznick, D.N. 2010. Ecology and evolution of swimming performance in fishes: predicting evolution with biomechanics. Pages 200-248 in P. Domenici and B.G. Kapoor, eds. Fish locomotion: an etho-ecological perspective. Enfield, Science Publishers

Types of Fishes and Habitats

- Shape and habitat are related and integral in survival.
- Tunas do not perform well on coral reefs



Types of Fishes by Swimming Habitat

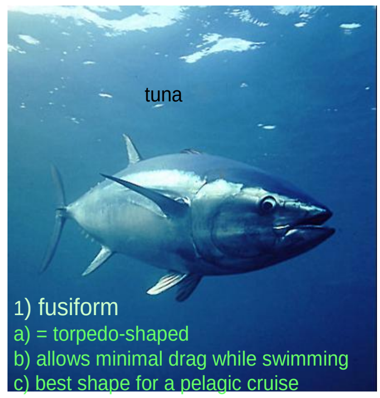
Cruisers:
Fish that swim almost continuously in search for food, e.g. tunas. Red Muscle- richly vascularized (blood-carrying capacity), rich in myoglobin (oxygen holder and transferor into the muscles active sites) able to sustain continuous aerobic movement.

Burst Swimmers:
These fish usually stay relatively in the same place such as most reef fish.

Cruisers – Ram Ventilation

Fusiform similar to a torpedo and cruises through the water at very high speeds.

Body shape



The <u>compressed shape</u> found on many reef fishes such as the butter fish

Agility for movement around the reef

support sudden bursts of acceleration

<u>elongated or attenuated</u>

long body trumpetfish, cornetfish, eels)

hide in holes in the reef

The eel allows wiggles into small crevices where it hunts prey. Also can hover motionless

The angler fish, scorpionfish are <u>depressed shape</u> and use "sit and wait" strategy of hunting

Terms Commonly Used for Direction

- Pitch - Moving up or down
  Yaw - Moving to the right or left
  Roll – Rotating for belly up.

Fins/ Propulsors

Provide control over movements by directing thrust, supplying lift and even acting as brakes. A fish must control its pitch, yaw, and roll.

Caudal fin-- provides thrust, and control the fishes direction

Pectorals-- act mostly as rudders and hydroplanes to control yaw and pitch. Also act as very important brakes by causing drag.

Pelvic fins-- mostly controls pitch

Dorsal/anal-- control roll

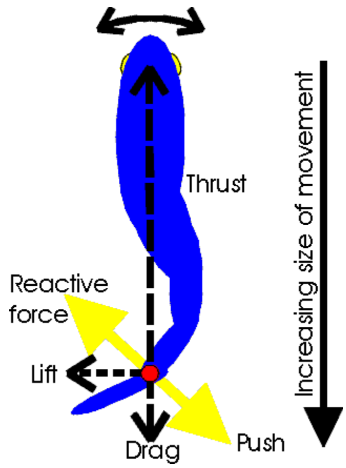


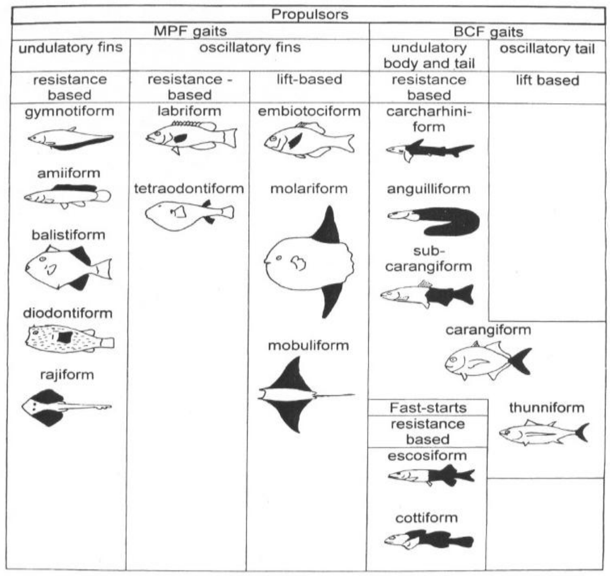
Diagram of forces when a fish swims.
Thrust- force in animal's direction
Lift- force opposite in right angles to the thrust
Drag- force opposite the direction of movement
** All lift forces cancel out over one complete tail stroke.

Drag is minimized by the streamlined shape of the fish and a slime fishes excrete from their skin minimize frictional drag and maintains laminar (smooth) flow of water past the fish.

Gaits

- Apply to fish swimming
- Beat patterns and body shape
- Median and paired fins **M P F** and body can be modified for swimming and use –
- **B**ody and **C**audal **f**ins **B C F** are used for more rapid propulsion

Median
paired



Body and
caudal

FIGURE 1. A hierarchical classification of fish propulsors, shown as shaded areas of the body and/or fins. Major subdivisions are based of gaits using the median and paired fins (MPF) which typically work together to propel fish at lower speeds, and the body and caudal fins (BCF) used for high-speed swimming and fast-starts. Within the major BCF and MPF categories, propulsors may undulate or oscillate, the latter either functioning like oars (resistance-based) or wings (lift-based). Named modes in these categories are based on the morphology of fins of fish which have become specialized for the use of a given propulsor in a limited locomotor repertoire. (Based on References 26, 27, 69, and 124).

Gaits combine propulsor, muscles and behavior

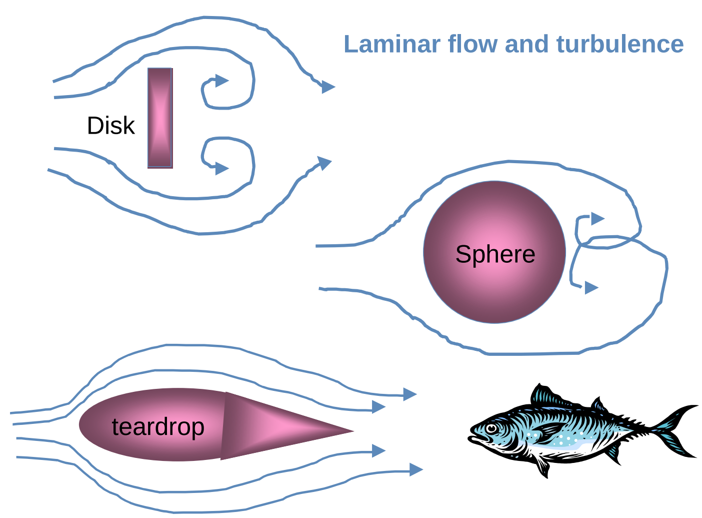
- Station holding
- Undulations
- Twitch
- Continuous
- Burst

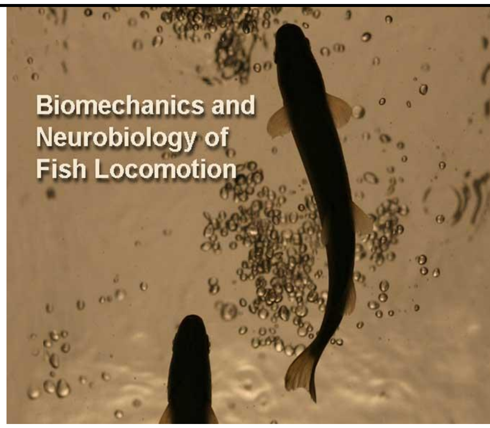
TABLE 1
Summary of "Design Features" Promoting Performance in Various Gaits and Swimming Behaviors[a]

Group	Propulsor Form	Muscle	Body Form	Other Traits
Cruiser/sprinter	Oscillatory lift-based propulsor to maximize thrust; narrow-based to orient propulsor to flow to maximize thrust. High aspect ratio to minimize induced drag.	~15% SO muscle mass for cruising. 20–50% FG muscle mass for sprints. Heat exchanger to trap muscle heat for thermoregulation.	Stiff, tear-drop body shape to minimize form drag. Circular cross section to minimize wetted area per unit body volume.	Negatively buoyant with stiff high-aspect-ratio paired fins to generate lift to control altitude. Large and viviparous or with rapid larval growth.
Accelerator (fast-start specialists)	Transient fast-start motions of propulsors with large body and fin depth over an elongate body to maximize acceleration reaction (low aspect ratio tail).	50–65% FG muscle mass to maximize force while minimizing nonmuscle inertial resistance.	Elongate, flexible body to bend into large amplitudes. Circular body cross section to minimize acceleration reaction resistance.	Large size to handle large prey. Usually neutrally buoyant.
Agility	Similar to fast-starts.	—	Gibbose form with large body and median fin depth to minimize inertia in rotation and sideslip.	—
Low-speed maneuverer	Large flexible fins to generate thrust oriented in all directions.	Amount of SO fin muscle limited by skeletal arrangements.	—	Neutrally buoyant.
Flow refugers	Fins used in behaviors to offset high lift in high-lift forms and to increase friction in high-drag forms.	—	Flattened, disc-shaped body in high-lift/low-drag forms. Depressed or fusiform body in high-drag/low-lift forms.	Increased proportions of high-density tissues.
Burrower	Elongate body to push against structures. Paired fins reduced or lost.	—	Elongate, highly flexible body.	—
Multitasker	Collapsible fins to change body/fin profiles.	Typically 5–10% SO muscle and 40–50% FG muscle.	Shape varies somewhat depending on dominant gait but generally fusiform.	Compensatory behaviors common.

[a] Data based on References 17, 68, 98, 111, 114, 117, 128, 129, and 138.

Laminar flow and turbulence





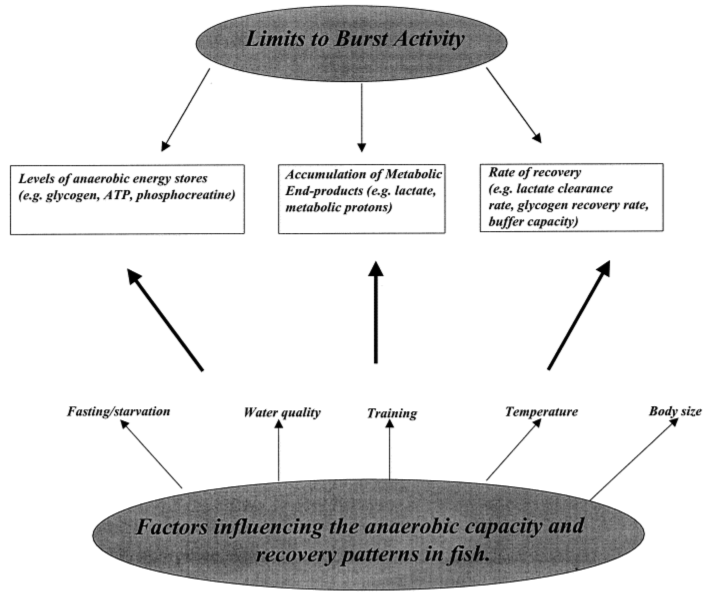
von Karman gait

http://www.people.fas.harvard.edu/~glauder/videos.htm

http://en.wikipedia.org/wiki/K%C3%A1rm%C3%A1n_vortex_street

Muscle Power and Swimming

- Slow oxidative (*SO* or red muscle)
  - Relatively low power output but aerobic and non fatiguing
- Fast glycolytic (*FG* or white muscle)
  - High power output but rapidly fatigues



Anoxia and Lac-ta-cidosis

- Tissue oxygen supply falls below metabolic demand
- Anerobic glycolysis with intermediary product is lactic acid
- Dissociates an equimolar amount of H+ ions
- Released H+ ions are buffered by non bicarbonate buffers or combine with bicarbonate before being eliminated from body by aerobic processing of lactic acid

Three mechanisms to restore pH during lactacidosis

- Adjustment of plasma CO_2
- Aerobic processing of lactic acid by breakdown to CO_2 and re-synthesis to glycogen
- Elimination of surplus H + ions from the body fluids

hypoxia

- Metabolism provides continuous load of CO_2
- Endogenous production of acid base relevant ions rises tremendously during extreme muscular activity and during extreme hypoxia.

Transepithelial acid base relevant ion transfer

- Main mechanism for fish acid base regulation
- Gill surface epithelium key for fish

Limits of Plasma Bicarbonate

- Extent of compensation is function of ratio between plasma and environmental bicarbonate concentration.

Energy Sources -1

- **Phosphocreatine**, **creatine phosphate** or **PCr** (**Pcr**), is a phosphorylated creatine molecule that serves as a rapidly mobilizable reserve of high-energy phosphates in skeletal muscle and brain.
- Phosphocreatine can anaerobically donate a phosphate group to ADP to form ATP during the first 2 to 7 seconds following an intense muscular or neuronal effort.

PCr

- Conversely, excess ATP can be used during a period of low effort to convert creatine to phosphocreatine. The reversible phosphorylation of creatine (i.e., both the forward and backward reaction) is catalyzed by several creatine kinases (CK).
- Phosphocreatine is synthesized in the liver and transported to the muscle cells, via the bloodstream, for storage

Energy Sources -2

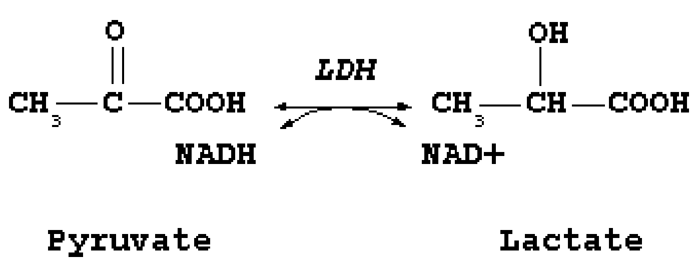
- Adenosine-5'-triphosphate (ATP) is a multifunctional nucleoside triphosphate used in cells as a coenzyme.
- "molecular unit of currency" of intracellular energy transfer. ATP transports chemical energy within cells for metabolism
- One molecule of ATP contains three phosphate groups, and it is produced by ATP synthase from inorganic phosphate and adenosine diphosphate (ADP) or adenosine monophosphate (AMP

Energy Released

- ATP + H2O → ADP + Pi $\Delta G^\circ = -30.5$ kJ/mol (−7.3 kcal/mol)
- ATP + H2O → AMP + PPi $\Delta G^\circ = -45.6$ kJ/mol (−10.9 kcal/mol)

Glycogen -3

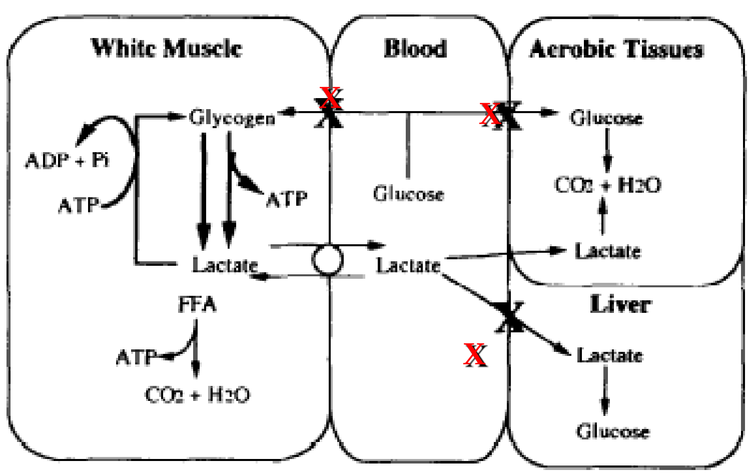
- Glycolysis
- The process converts one molecule of glucose into two molecules of pyruvate (pyruvic acid), generating energy in the form of two net molecules of ATP.
- Glucose + 2 NAD+ + 2 Pi + 2 ADP → 2 pyruvate + 2 NADH + 2 ATP + 2 H+ + 2 H2O + heat



Contribution of blood glucose and lactate to muscle glycogen re-synthesis during recover from exhaustive exercise

Hrs after exercise	Glycogen change (μ mol/g)	Resynthesized from blood glucose (%)	Resynthesized from blood lactate (%)
0-2	2.23	0.1	6.2
2-4	0.51	0.1	47.8
4-6	1.62	0.4	3.7

From Milligan 1996



The **<u>Lactate</u>** **is recycled without the Liver, and stays in muscle in situ glycogenesis**

Understanding of recovery

- Still not well known
- Lots of studies of factors affecting this
- Training in fish?
- Trials in field vs lab

Tufts et al. 1991

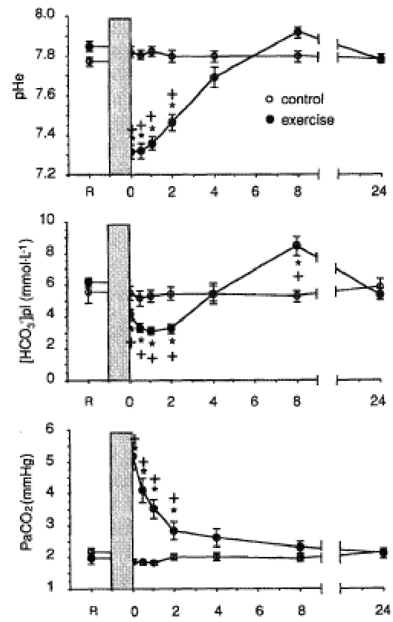
- Wild Atlantic salmon lactacidosis
- Exercised to exhaustion
- Acid base regulation observed

Exhaustive Exercise in Atl. Salmon :
Acid-Base Reg and blood Gas Transport (Tufts et al)

- Doral cannula
- 48 h recovery
- Baseline
  - pH, CO2, O2, PO2, hct, plasma C02, lactate, erythrocyte pH,
- Exhaustion by chasing

Measures

- pH – direct
- O2 - direct
- Erythrocyte Hb
- CO2 blood and plasma – GC
- Arterial CO2 and plasma bicarbonate – calculated
- Nucleotide triphosphate NTP = adenosine triphosphate (ATP), guanosine triphosphate (GTP), cytidine triphosphate (CTP), thymidine triphosphate (TTP) and uridine triphosphate (UTP) *ENERGY*

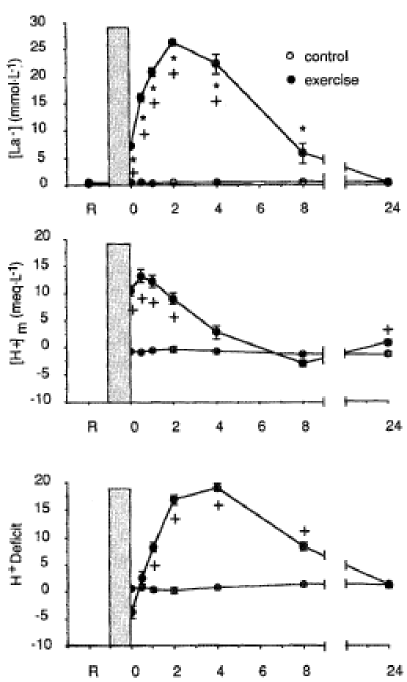


hours

extracellular pH

Plasma bicarbonate

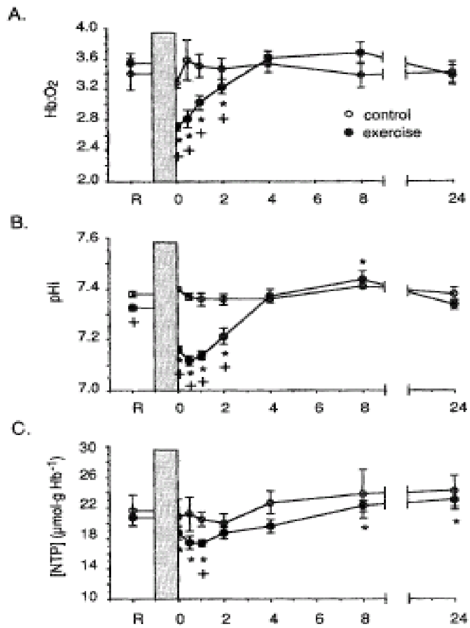
Arterial CO2 tension



Lactate

Metabolic Proton load H+

H+ deficit



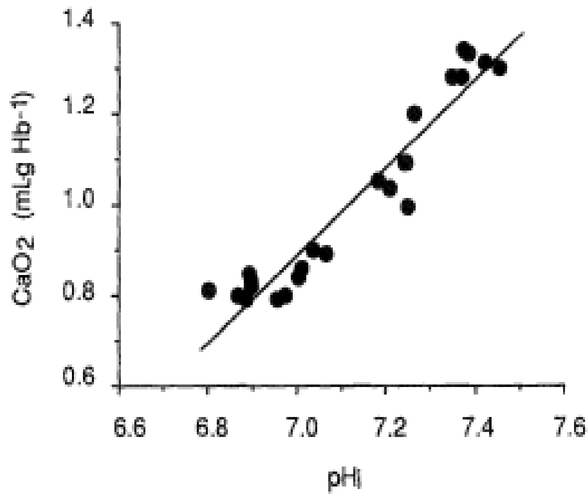
Hemoglobin: oxygen carriage

Erythrocyte pH

Erythrocyte NTP (nucleotide triphosphate) concentration

TABLE 1. Effect of exhaustive exercise on hematocrit, Po_2, and O_2 content (CaO_2) in *S. salar* at 18°C. Values are means ± standard error (control, N = 4; Exercise, N = 6). Asterisk denotes significant ($p < 0.05$) difference from resting value; plus sign denotes significant ($p < 0.05$) difference from control value.

	Rest	0 h	0.5 h	1 h	2 h	4 h	8 h	24 h
Hematocrit (%)								
Control	25.4 ± 3.8	25.2 ± 3.5	24.5 ± 4.7	25.9 ± 3.4	24.2 ± 3.5	21.6 ± 3.5*	20.6 ± 4.8*	19.4 ± 3.4*
Exercise	29.5 ± 2.7	32.7 ± 1.9	38.2 ± 2.1*	37.9 ± 1.4*+	35.6 ± 1.6+	29.9 ± 1.9	21.4 ± 1.9*	20.0 ± 3.0*
Po_2 (mmHg)								
Control	87.2 ± 5.4	86.7 ± 4.9	87.8 ± 3.9	87.9 ± 3.6	90.9 ± 4.7	92.4 ± 4.4	88.0 ± 6.0	81.9 ± 6.1
Exercise	89.4 ± 2.5	77.3 ± 4.0*	84.9 ± 7.3	98.6 ± 3.7*	92.4 ± 4.8	87.5 ± 4.6	95.8 ± 2.3	94.7 ± 4.1
CaO_2 (vol %)								
Control	10.4 ± 1.6	9.7 ± 1.2	10.5 ± 2.4	10.1 ± 1.4	9.8 ± 1.5	8.7 ± 1.4*	8.2 ± 2.0*	8.2 ± 1.4*
Exercise	12.0 ± 0.6	9.7 ± 0.6*	11.6 ± 0.7	12.0 ± 0.6	11.8 ± 0.5	11.5 ± 0.6	9.4 ± 0.7*	8.4 ± 1.1*



Arterial oxygen versus erythrocyte pH

Conclusions

- Burst activity associated with marked acidosis
- Most severe 2 h immediately following exercise
- RBC sensitive to adrenergic stimulation in vitro
- Perhaps RBC are aged in migrating fish
- Spleen may be more important than regulation of pH following exhaustive exercise in migrating Atlantic salmon with increase number rbc
- Delayed mortality in catch and release fishing??

Handouts for summary of mechanisms on class web

Exercise

Hypoxia

James D. Kieffer , Andrew M. Rossiter , Christine A. Kieffer , Kevin Davidson & Bruce L. Tufts. 2011.

- *Physiology and Survival of Atlantic Salmon following Exhaustive Exercise in Hard and Softer Water:Implications for the Catch-and-Release Sport Fishery*
- North American Journal of Fisheries Management, 22:1, 132-144

Hard water versus soft water systems

- Hard vs soft
- 40 mg/L versus
- 100 mg/L CaCO3

- 300–500 g Atl Salmon

Mean (±SE) arterial blood plasma **(A)** [lactate] and **(B)** $[H_m^{+}]$

5 min of exhaustive exercise (stippled bar)

Asterisks denote a significant difference ($P < 0.05$) between resting and postexercise values; plus signs indicate a significant difference ($P < 0.05$) between the fish in hard versus softer water for a given hour in the experiment.

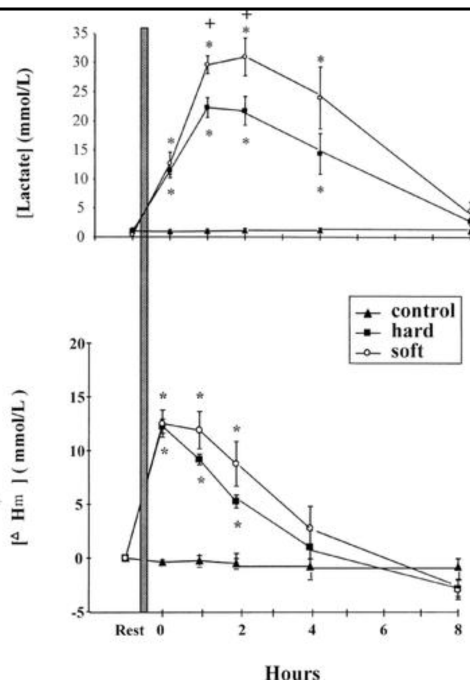
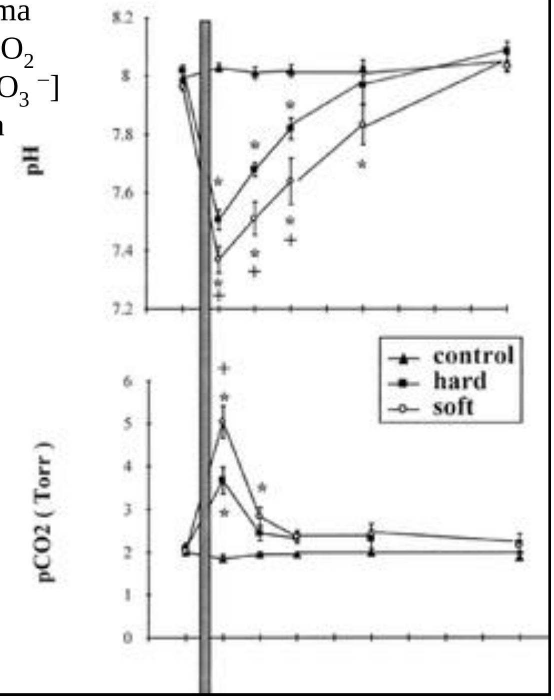


Figure 2. Arterial blood plasma **(A)** pH, **(B)** arterial plasma CO_2 tension (Pa_{CO2}), and **(C)** [HCO_3^-] in cannulated Atlantic salmon recovering from 5 min of exhaustive exercise.



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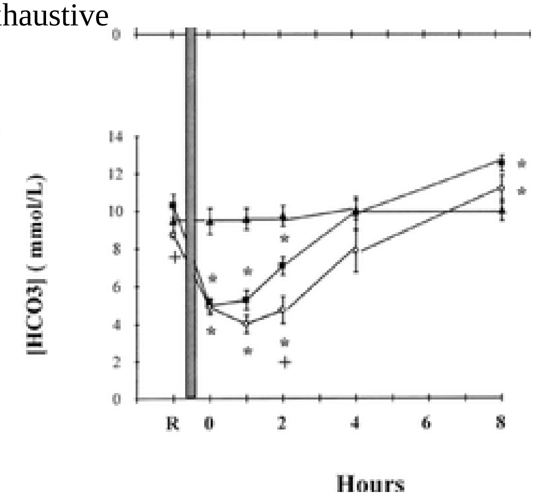


Figure 3. Mean (+SE) white muscle **(A)** adenosine triphosphate [ATP], **(B)** phosphocreatine [PCr], and **(C)** glycogen in Atlantic salmon before exercise, following 5 min of exhaustive exercise after 4 h recovery.

Plus signs indicate a significant difference ($P < 0.05$) for fish in hard versus softer water for a given hour in the experiment.

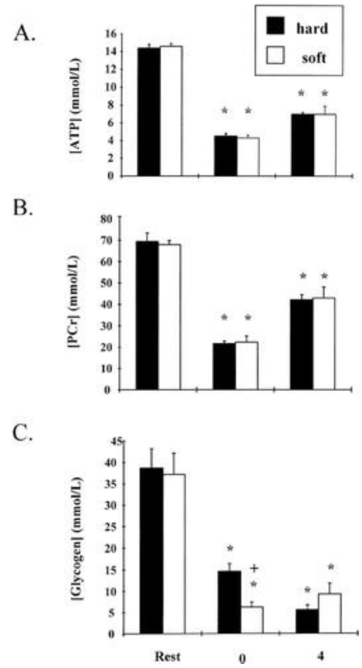
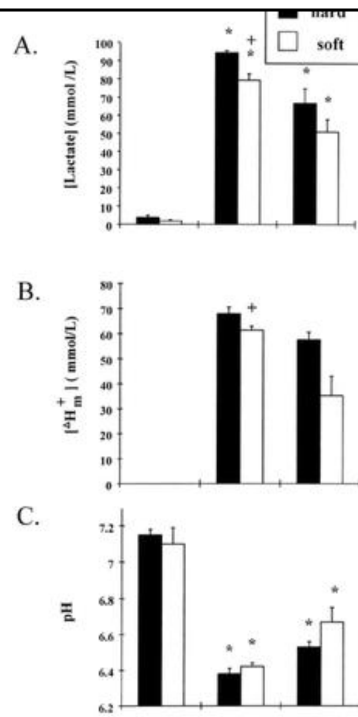


Figure 4. Mean (+SE) white muscle **(A)** [lactate], **(B)** [H_m^+], and **(C)** pH I

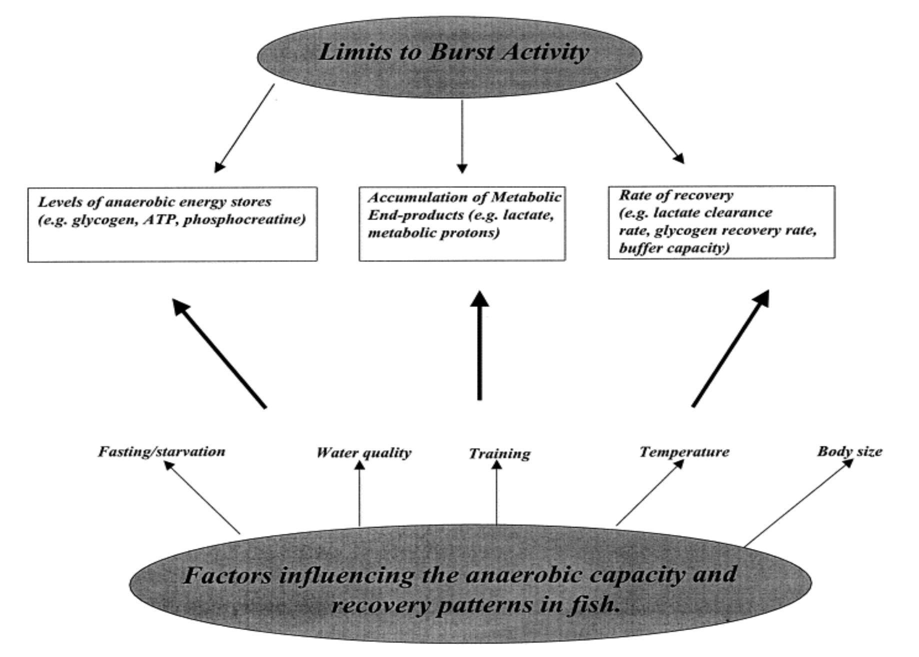
Asterisks denote a significant difference ($P < 0.05$) between resting and postexercise values;

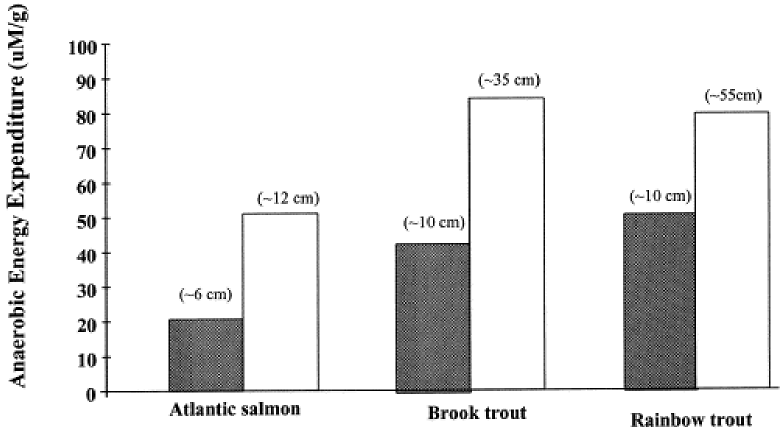
Plus signs indicate a significant difference ($P < 0.05$) for fish in hard versus softer water for a given hour in the experiment.



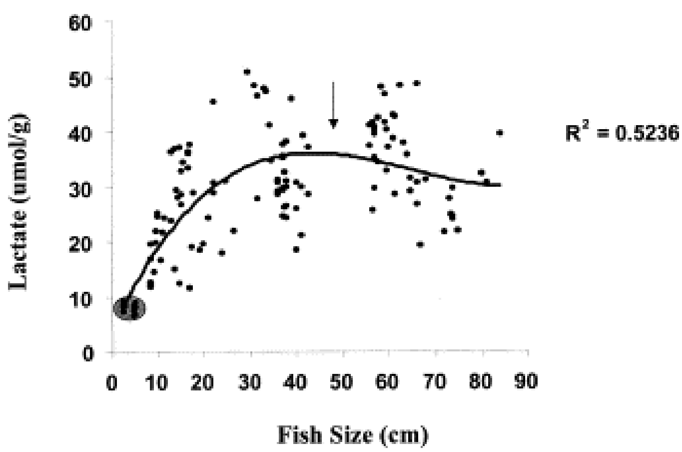
Limits to exhaustive exercise in fish: review

- James D. Kieffer – lots of contributions to this subject
- Evaluates effects of body size, temperature, fasting vs starvation and training





Body size, anerobic energy expenditure



Size versus maximum lactate production

Allometric relationships

- http://home.fuse.net/clymer/minor/allometry.html
- Web cite to calculate this given coefficients

What is this equation

- $Y = Y_o * M^b$
- What is this in fish?
- Magic coefficients between .7 – .8?

Species Factors in Maximum Lactate

- Again, limited comparisons, but generally bottom fishes have less capacity to produce this.

- Review tables in Kieffer

Maximum elevation in lactate micro moles/g

Species	Muscle lactate	Reference
Adult Rainbow trout (*O. mykiss*)	41 ± 2.6	Schulte et al., 1992
	~ 30	Kieffer et al., 1994
Adult Atlantic salmon (*S. salar*)	~ 45	Wilkie et al., 1997
	~ 37	Booth et al., 1995[a]
	~ 25	Brobbel et al., 1996[a]
[illegible]	[illegible]	[illegible]

Maximum elevation in micro moles/g

Adult Smallmouth bass (*Micropterus dolomieu*)	~18	Kieffer et al., 1995[a]
Yellow perch (*P. flavescens*)	~24	Schwalme and Mackay, 1991
Roach (*Rutilus rutilis*)	6 ± 1	Dalla Via et al., 1989

Exhaustive exercise

- Other factors such as training, fasting
- What about multiple challenges?

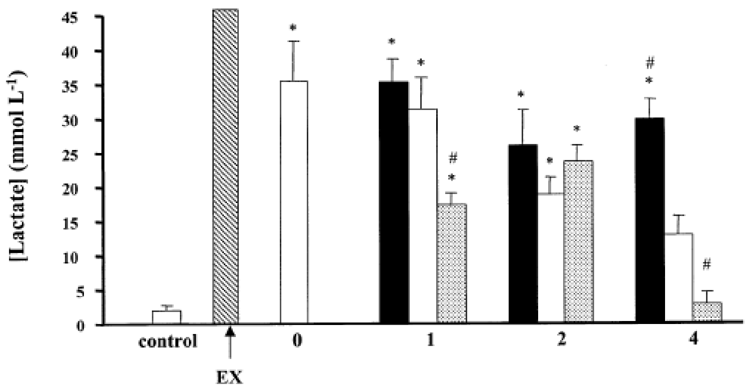
Temperature of acclimation affecting muscle lactate?

- Temperature influences the recovery rates of most metabolites, but not PCr .
- Recovery rates for ATP and glycogen are slower at cooler temperatures but there are limits

Temperature Effects

Species	T °C	ΔLac⁻	ΔPCr	ΔATP	AEE[b]
Rainbow trout (*O. mykiss*)	5	30	30	2.5	~78
	18	30	40	4.3	~89
Atlantic salmon (adult) (*S. salar*)	12	36	29	6.6	~90
	18	34	13	8.2	~72
	23	35	17	5.5	~75
Atlantic salmon (juvenile) (*S. salar*)	6	40	27	7	~94
	18	41	23	6	~91
Herring (larvae) (*Clupea harengus* L.)	5	5	15	2	~25
	12	6	15	2	~26

Recovery of Lactate at 6, 12, and 18°C



30 g Atlantic salmon exercised at 12 °C

Temp effects are measured

- Cardiac output and rate
- Most salmonid studies agree acclimation temperature does not influence maximum lactate, or the total energy release.
- However, most studies of bioenergetics have concentrated on aerobic performance, not anaerobic situations.

Temperature Effects Physiology at many levels

- Individual
- Population
- Community
- Evolutionary processes

Ecosystem and Community

- Change in quality and availability of foods, predators, timing of spawning events, migrations

Temperature and Fish Physiology

- Thermal biology dominated by constraints of respiration
- Limited solubility of O_2 in H2O
- High heat capacity of water ensures blood is equilibrated with water
- Thus heat generated by metabolism is carried to gills and lost to environment.

- Temperature determines rate of chemical reactions
- Temperature dictates point of equilibrium in reactions
- Temp affects structural flexibility components for protein and biological membranes
- Thus, significant changes in body temperature pose a serious challenge to maintenance of physiological functions

- Some (very few) fish are endothermic
- Most fish are isothermal with environment and must contend with variable body temperatures
- However, fluctuations are not exceptionally large compared with what can happen in the air

Endothermic fishes

- One group of large marine fishes
  - Mackerels, tunas, bonitos, billfishes, and some sharks (white and mako)
  - Characterized by large body size (thermal inertia)
  - Two patterns – whole body (tunas)
  - Regional endothermy – billfish heat brain and eye

Modification in endothermy

- Movement red muscle mass internally (not the characteristic of outer layer)
- Change in circulatory system and use of rete mirabile (parallel intermingled arterioles and venules).

Significance

- Capacity for fast sustained swimming
- Elevated temp accelerates myoblobin-mediated diffusion of oxygen, rate of oxygen delivery to mitochondria
- May aid clearance of lactate. Typical teleosts require 12 – 24 h versus 2 – 3 h in tunas

Poikilothermy- Ectothermy

- Most typical for fishes (inverts, reptiles, amphibians)
- Ambient conditions dictate temperature
- Behavioral adjustments (thermal refugia for summer and winter conditions)

Adjustments to Temperature Changes

- Some adaptation such as increasing surface circulation
- Evolutionary adaptation to specific environments
- Evolutional distinctions in tolerance
  - Eg polar fishes versus desert fishes
  - Antifreeze proteins

Feeding , swimming, and O2 concentration

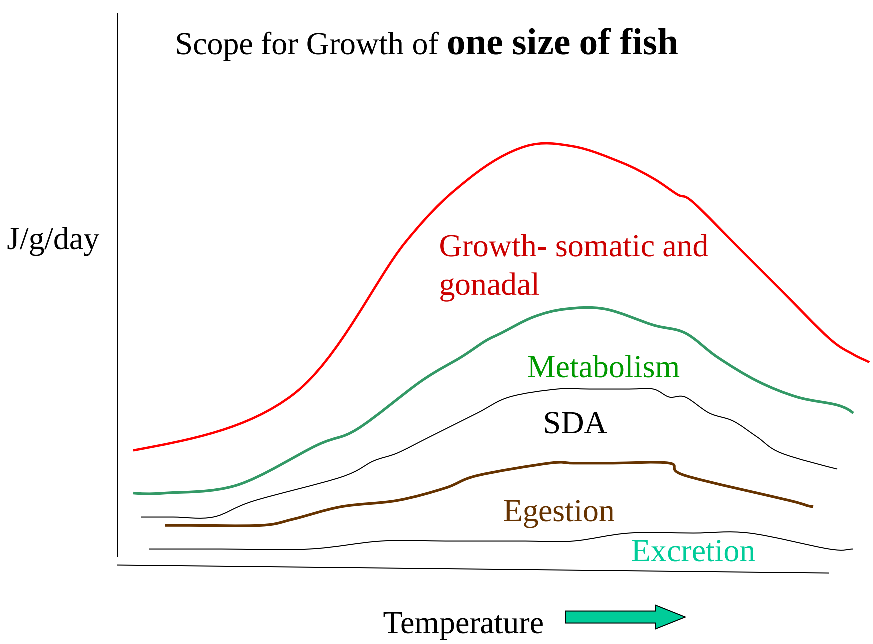
- Temperature is a component of the metabolic rate and oxygen consumption
- Warmer water temperatures increases O2 consumption rates by increasing the metabolic rate.

Optimal Temperatures

- Species and life history stages (size) will have different optimal temperatures
- Selection on species to be as efficient with resources, but other factors affect this

BioEnergetics

- Study of pathways and mechanisms through which energy enters, is stored, used, and lost from organisms for growth, maintenance, and reproduction
- C = Growth + (Metabolism + SDA) + F(egestion) + U (excretion)
- Specific dynamic action = energy lost during chemical transformation of food into energy



Limitations

- SDA and M usually measured as depletion of oxygen in closed respiratory chambers
- The activity level needs to be considered in these equations
- Generalization for specific size classes is important!!!
- Allometric relationships – need to understand relationships

Preparation for Discussions

- Read all papers, discussion on Tuesday or two studies of physiology
- Thursday, discussion of fishing in an ethical context. Be prepared to challenge yourself and others in this discussion.
- Then our first round table exam follows.