Ecosystems & Ecophysiology – Lecture 10

Introduction to ecophysiology

Objectives

1. Understand the effects of temperature on enzyme-catalysed reactions.

2. Know the differences between exponential and logarithmic equations, and how their parameters may be found from suitable plots.

3. Know the temperature quotient Q_{10}, and how this may be calculated over different temperature intervals.

4. Understand the terms ectotherm, endotherm, heterotherm, thermoconformer and thermoregulator.

5. Know the different processes of heat exchange between an organism and the environment.

References

The recommended book for the second half of the course is:

Schmidt-Nielsen, K. (1997). Animal physiology: adaptation and environment (5th edition). Cambridge University Press.

Material on plants and microorganisms, and other animal examples, can be found in the books on aquatic ecology listed for the first half of the course, and in the following book (most of which is too advanced for this course):

Hochachka, P.W. & Somero, G.N. (2002). Biochemical adaptation: mechanism and process in physiological evolution. Oxford University Press.

You will be expected to understand the principles from the Animal Physiology section of the level 1 course **Life Processes**. The relevant lectures are available on Blackboard ("Course Information" folder).

Introduction to ecophysiology

Ecophysiology half of the course, look at adaptations to three physical variables important in aquatic systems – temperature, oxygen & salinity

As expected from the set book, mostly animal examples. Plant physiology at this level is mostly of terrestrial flowering plants. Some plant & microorganism physiology in aquatic systems included where possible

Temperature and life

Temperature affects essentially every aspect of an organism's physiology. Importance shown by clear latitude limits to distribution of most species

■ Temperatures in the biosphere range from just > 100^{o}C in boiling springs & the occupied parts of hydrothermal vents, down to –80^{o}C on land at high latitude & altitude

Thermophilic archaea > 100^{o}C, most tolerant is *Pyrolobus fumarii* from hydrothermal vents, can complete life cycle at 113^{o}C, optimum 106^{o}C

Cyanobacteria in hot springs to 89^{o}C. Note green colour in stream leading from hot spring (Yellowstone), not in spring itself which is too hot

■ Much lower range of temperature in most aquatic environments. Latitudinal gradient of mean temperature in surface water of oceans

Just >25^{o}C in tropics. Just < 0^{o}C at poles, water temperature stabilised by formation of ice. High heat of fusion of water prevents temperatures falling to the very low levels experienced on land

■ Standard abbreviations are T_b for body temperature, and T_a for ambient (environmental) temperature

Most animals restricted to T_bs from a few degrees below zero to about 50^{o}C (few polychaetes at hydrothermal vents to 80^{o}C). Similar limits in flowering plants. Mosses to 51^{o}C, some green algae up to 75^{o}C

Dormant organisms more tolerant, bacterial spores to 120^{o}C, dry mosses to 110^{o}C, dry fly larva to 102^{o}C. Rotifers & tardigrades may be alive after freezing in liquid helium at –269^{o}C

No single species is active at temperatures over the whole range, & many species have narrow tolerances

Environments differ in both mean & variability of T_a. Extreme temperatures & high variability are both major physiological stresses

Aquatic environments have more stable temperatures due to high specific heat capacity & thermal inertia of water. Annual variation in channel sea water is much lower than daily variation of desert air

■ Temperature increases rate of most physiological processes over a moderate temperature range. E.g. rate of enzyme-catalysed reaction

Relationship is called a rate-temperature or R-T curve. Rate decreases at high temperature as enzyme begins to be denatured, loses specific folded structure & so catalytic activity

■ Up to this point rate usually increases exponentially with T_b, i.e. where the increase occurs as a constant proportion rather than a constant amount

Exponential increase can be expressed as the Q_{10} – the temperature quotient for a 10°C increase. This is usually between 2 & 3 for enzyme catalysed reactions, & so for physiological rate (i.e. $time^{-1}$) processes

■ R-T curve is thus an exponential curve on a graph with linear axes, but a straight line on a semi-log graph with a log rate axis. E.g. data for oxygen consumption of Colorado beetle

Equations & graphs
Some technical points before looking at temperature. Use examples of metabolic rate, a measure of the overall level of physiological activity of an organism, like GNP for economic activity of a country

For aerobic organisms, metabolic rate is measured as consumption of O_2. Can be converted to rate of energy use, units of $\mu l\ O_2\ g^{-1}\ h^{-1}$ or $J\ g^{-1}\ h^{-1}$ etc

1. Exponential equations. For example R-T curves, are of the form **$y = a.b^x$**

Which can be converted to the logarithmic form **$\log y = \log a + x.\log b$**

In this case log y is a linear function of x, and plotting log y on x (on semi-log graph) gives a straight line. Why do this? Two reasons:

a) Deviations from the exponential curve can be seen more clearly. Oxygen consumption of the Colorado beetle clearly increases less at higher temperature

b) Because the variability of the data (e.g. the SD) is proportional to the mean. Log transformation allows all data to be shown to the same level of accuracy on a graph

Also necessary for statistical testing. Data for many physiological rate processes are skewed & must be log-transformed before analysis

Parameters of the exponential equation can be estimated from the plot:
The intercept is log a, so a = the antilog of the intercept
The slope is log b, so b = the antilog of the slope

■ **2. Logarithmic equations**. These are superficially similar to exponential equations, of the form **$y = a.x^b$**

Which can be converted to the <u>logarithmic form</u> **$\log y = \log a + b.\log x$**

In this case log y is linearly related to log x, and the data are plotted on log-log axes, i.e. <u>log y on log x</u>

Parameters of the logarithmic equation can also be estimated from the plot. The intercept is log a, so <u>a = the antilog of the intercept</u>, as before

But in this case the slope is b (not log b), so <u>b = slope</u>, not the antilog of the slope as in the exponential curve

■ These graphs are used extensively in studying <u>allometric</u> relationships, comparing physiological variables with body size. E.g. metabolic rate of birds (note energy units)

In this case the slope is < 1, so metabolic rate increases less quickly than mass. If the slope = 1 the relationship is linear. If slope > 1 then y increases more rapidly than x, e.g. <u>slope = 3 for a cubic</u> relationship

Even if the slope = 1, logarithmic axes are useful to display <u>wide range</u> of values. In this case metabolic rate varies by 1000 x, & mass by 10,000 x

■ **3. Calculation of Q_{10}**. Q_{10} is the <u>proportional increase</u> in rate over a 10°C interval, i.e. doubling gives $Q_{10} = 2.0$

So for a <u>10°C interval</u> **$Q_{10} = R_{T+10} / R_T$**
where R_T is the rate at temperature T

Q_{10} can be calculated for <u>other temperature ranges</u> (T_1 to T_2), provided they are wide enough to give reliable information:

$$Q_{10} = (R_2 / R_1)^{10/(T2-T1)}$$

where R_2 is the rate at the higher temperature T_2 etc

If T_2 is 10°C higher than T_1 the <u>exponent = 1</u> and this equation reverts to the simpler one above

Most useful when <u>log-transformed</u> **$\log Q_{10} = (\log R_2 – \log R_1) . 10 / (T_2 – T_1)$**
And Q_{10} = antilog ($\log Q_{10}$)

■ Q_{10} is usually <u>between 2 & 3</u> for enzyme-catalysed reactions. Well known, but needs explanation, because the increase in rate is much larger than the increase in the mean kinetic energy of the reacting molecules

Kinetic energy (of molecular movement) increases with temperature. <u>Activation energy</u> ΔG^* is the energy required for a reaction to occur. If kinetic energy of molecules > ΔG^* they will react

Enzymes are catalysts because they lower ΔG^*, so the reaction is more likely to proceed. Increase reaction rates by 10^3 to 10^{17} x

Overall free energy change ΔG^o is the same for both catalysed & uncatalysed reactions. This is the difference in free energy between substrates & products, independent of the route of reaction

■ Temperature is a measure of the mean kinetic energy of molecules, but reaction velocity depends not on the mean but on the proportion of molecules with energy > ΔG^*

A small % change in mean kinetic energy may give a much larger change in the proportion of molecules with energy > ΔG^*

At biological temperatures a 10^oC change gives only a 3% change in mean kinetic energy. Mean energy is directly proportional to absolute temperature (Kelvin): $25^oC \approx 300$ K and 10/300 = 3%

Although mean energy only increases by 3%, the proportion of molecules that are reactive (with energy > ΔG^*) may increase by 2-3 x

In contrast purely physical processes such as diffusion only increase with the mean kinetic energy of the molecules & have much lower Q_{10}s, close to 1

Terminology

■ Several schemes used to describe the thermal relations of organisms, especially animals. Two that you will see, but don't use:

1. Warm-blooded – birds & mammals
   Cold-blooded – everything else

But many "cold-blooded" animals may have high T_bs, > 40^oC, higher than some warm-blooded animals

2. Homeotherm (or homoiotherm) – constant T_b
   Poikilotherm – changeable T_b

Same taxonomic split, homeotherms = birds & mammals, poikilotherms = everything else. But in a stable thermal environment a "poikilotherm" will have a very constant T_b

E.g. deep ocean invertebrate, T_b shows less variation than most homeotherms, which may change by a few degrees

Can avoid some of these problems by subdividing poikilotherms into:

- Stenothermal – narrow range of T_b
- Eurythermal – wide range of T_b

■ 3. Endotherm – internal source of heat (metabolic)
   Ectotherm – external source of heat

Don't use exotherm (Mc Farland, *Animal Behaviour*) instead of ectotherm, confuses with exothermic chemical reactions (which give out heat)

Endotherms sometimes divided between:
- Classic endotherms – birds & mammals (also termed euthermic)
- Non-classic endotherms – a few plants, insects, fish & reptiles

4. Thermoregulator – T_b is independent of environment
   Thermoconformer – T_b is determined by environment

■ Plot of T_b on T_a has slope of zero for perfect thermoregulator – independent of environment

Plot of T_b on T_a has slope of 1.0 for perfect thermoconformer – determined by environment

■ No single best way of classifying thermal relations of organisms, but a combination of 3 & 4 is most useful:

Thermoconforming ectotherms. All microorganisms, all but a few plants, most animals – all aquatic & most terrestrial invertebrates, most fish & amphibians, some reptiles.

These have to cope with extremes & changes in T_b (Lectures 12 & 13)

Thermoregulating ectotherms. Some amphibians & terrestrial invertebrates, most reptiles. Use external heat to minimise fluctuation of T_b. Some intertidal animals (Lecture 11)

Endotherms are usually also thermoregulators. Birds & mammals, a few plants, insects, fish & reptiles. Aquatic examples in Lecture 11

■ One other term, heterotherm: variable between endotherm & ectotherm:

a) Temporal (variable in time). Classic endotherms that lower T_b when torpid. E.g. daily torpor in birds, seasonal hibernation in mammals. Not found in aquatic systems as T_a more stable than on land

b) Regional (variable in space). Endotherms that increase temperature of only part of the body, e.g. brain or muscles in fish (Lecture 11)

Processes of heat exchange

■ Heat energy is exchanged between an organism & the environment. Similar diagrams in most animal physiology books, but some variations (e.g. neglect conduction if based on standing mammal). Components:

1. Direct solar radiation is mostly short-wave (visible light), as is radiation reflected from the ground. Some short-wave radiation is reflected from the animal, not absorbed

2. Long-wave radiation comes from objects that have absorbed short waves, heated up, & re-radiated the energy as infrared. Animal gains energy by infrared from the ground, but loses energy by itself radiating infrared

3. Particles in the atmosphere, including water vapour, reflect short waves, or absorb them & radiate infrared. Diffuse radiation from the sky thus includes both short-wave & long-wave

4. Conduction from physical contact, especially with ground or water. Direction depends on temperature difference – often to the animal in ectotherms, from the animal in endotherms

5. Convection. Heat exchange with a moving fluid medium. Can be either:

a) Forced – wind or water currents, internally by blood
b) Free – in still air or water, fluid movement caused by temperature & thus density changes

6. Evaporation always produces heat loss. Can be both cutaneous (e.g. sweat) & respiratory (water vapour from lungs)

May be condensation on cold plants or animals giving heat gain, but more significant for water balance, e.g. fog on Namib beetles

7. Metabolic heat production. Always produces heat gain, but only physiologically significant at high metabolic rates