‘Normal Physiology’, Acclimation, and Stress

Organisms in Ecosystems

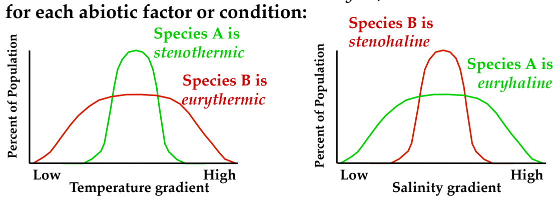
- Organisms must reconcile their needs with what the environment provides
  - Organisms need a fairly constant internal environment. Because of entropy, organisms must acquire and use energy to maintain *homeostasis*
  - Maintenance of homeostasis is possible only under a certain range of conditions (*tolerance limits*). These tolerance limits vary with the individual and over time and space
  - Organisms cannot do equally well in different environments (habitats). Distribution of organisms in habitats reflects environmental variation and evolutionary history
- Environmental challenges are countered by *adaptations*: inheritable traits that influence fitness
  - Adaptations are the product of *natural selection*
  - Organisms must be adapted to abiotic conditions within the habitat, e.g., temperature, moisture, light, radiation, salinity, pH, and gravity
  - Organisms generally live in habitats together with organisms with similar requirements. Must be adapted to these *competitors*
  - Organisms must also be adapted to *diseases, predators, parasites*, etc.

Limiting Factors

- When limits for one or a few factors that affect homeostasis are approached, those factors generally become most important in determining survival, that is, they become *limiting factors*
  - Proposed by Liebig (1840) as “ The Law of the Minimum”: the growth and/or distribution of a species is dependent on the one environmental factor that is in shortest supply
  - Important in understanding physiological limits on animal distribution and abundance
- The exception is when one factor changes the tolerance for limitation of another (e.g., temperature and salinity), or when a second substance can substitute for another when availability of the first is limited (e.g., Sr for Ca in coral skeletons)

Tolerance Range

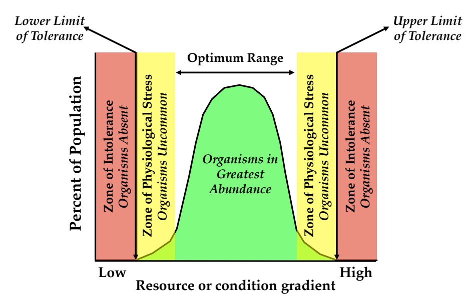
Can be narrow (‘*steno-*’) or broad (‘*eury-*’), and is different for each abiotic factor or condition:



- Tolerance ranges differ both within and between populations (populations with fixed and genetically-determined tolerances are called *ecotypes*)
- The tolerance range for one factor may affect tolerance ranges for others
- Tolerance ranges can change with different seasons, lifestyle stages, condition, age, etc.

Tolerance Range

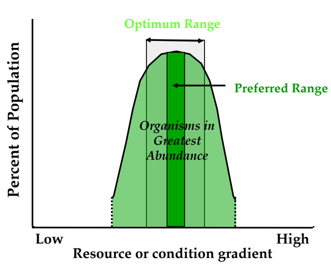
Shelford (1940) *Law of Tolerance* - For each abiotic factor or condition, there is a range within which an organism can survive and reproduce



Zones of Tolerance Range

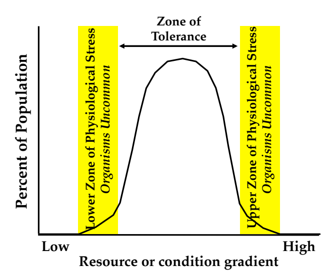
Zone of tolerance - central range at which the animal is most comfortable

- Within this range, there is often a narrower *optimal range* where the population does very well, and sometimes a *preferred range* that is actively sought out/and or competed for by individual organisms



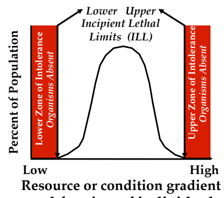
Zones of Tolerance Range

Zone of tolerance is bounded by an *upper* and *lower zone of physiological stress* (or *resistance*), within which the organism can survive for an indefinite period



Zones of Tolerance Range

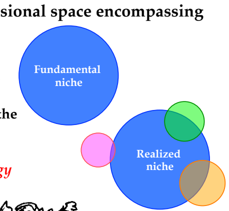
The bounds of the *upper* and *lower zone of intolerance* are determined by the *upper* and *lower* *incipient lethal limits* (ILL), respectively:



- ILL is the level where a stated fraction of individuals in a population (usually 50%) when brought rapidly to this level from a different level, will die within an indefinitely prolonged exposure
- ILL is not fixed, determined by previous acclimation history of the organism
- Acclimation has limits, however, and eventually the upper and lower *ultimate incipient lethal limits* are reached

Niches

- A 'living space' encompassing all of an organism's tolerance ranges defines the organism's 'profession' or *niche*
- G.E. Hutchinson described the niche as an "*n*-dimensional hypervolume": an imaginary, multi-dimensional space encompassing all of an organism's required resources and conditions
  - *Fundamental niche*: the full range of conditions to which the organism is or can be adapted
  - *Realized niche*: the (always) *smaller* portion of the fundamental niche that the organism actually gets to use

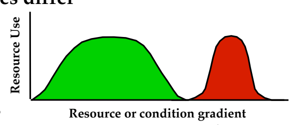


Humans are unique in that their use of technology has allowed then to hugely expand their niche

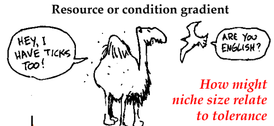
- Different species (*must*) occupy different niches
  - For example, some plants grow only on shady, moist, poorly-drained sites, while others live only on sunny, well-drained hillsides

Niche Size and Overlap

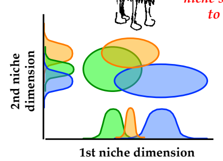
- Niche sizes of different species differ
  - Species with wide (broad) niches are *generalists*
  - Species with narrow niches are *specialists*, e.g., starlings in England eat only the ticks off of sheep and deer



- *Niche overlap* occurs whenever two or more organisms use the same resource. May result in:
  - *Intraspecific competition* if organisms are the same species
  - *Interspecific competition* if organisms are different species

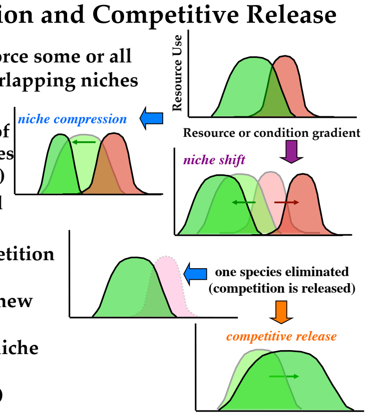


How might niche size relate to tolerance ranges?



Niche Reduction and Competitive Release

- Competition may force some or all organisms with overlapping niches to:
  - Decrease the size of their realized niches (*niche compression*)
  - Alter their realized niches (*niche shift*)
- In contrast, if competition is released (e.g., if a species colonizes a new habitat with no competitors), then niche size may expand (*competitive release*)



"Normal" Physiology

- When environment is such that the organism is within tolerance limits for all factors, *"normal" physiology* occurs and the organism is free of *stress*
- Often measured along a continuum from the molecular (e.g., induced proteins) to the ecosystem level (e.g., shifts in respiration:production or nutrient cycling)
- Most often, a measurement of "stress" is implied for any significant shift in a quality regardless of the level examined
  - *Direct indicators* (e.g., change in hormone levels)
  - *Indirect indicators* (e.g., increased intensity of parasite infection)

What Is Stress?

Definitions vary, even at the level of the individual

Adams (1990) compiled the following definitions:

- "…the sum of all physiological responses that occur when animals attempt to establish or maintain homeostasis, the stressor being an environmental alteration and stress the organism's response"
- "…adaptive physiological changes resulting from a variety of environmental stressors"
- "…a diversion of metabolic energy from an animal's normal activities"
- "…the sum of all physiological responses by which an organism tries to maintain or reestablish normal metabolism in the face of chemical or physical changes"
- …alteration of one or more physiological variables to the point that long-term survival may be impaired"
- …the effect of any environmental alteration that extends homeostatic or stabilizing processes beyond their normal limits"

What Is Stress?

"Everybody knows what stress is and nobody knows what it is"
– Hans Selye (1973)

- **Selye (1956, 1973) developed the concept of stress as: "…the state manifested by a specific syndrome which consists of all the nonspecifically induced changes within a biological system".**
- **Selye also clearly stated that stress is characterized by a specific syndrome in response to an *external agent***
- **Stress is achieved during any of a variety of activities, including many non-detrimental activities, e.g., exertion.**
- **Stress is also a distinctive or specific suite of responses that are beneficial or compensatory.**

What Is Stress?

In these definitions, "stress" is used to identify:

- **A response**
- **A characteristic or specific response**
- **An effect**
- **An external factor causing a response or effect**

In this course:

- **The external effect will be termed the *stressor***
- **The response is *stress***

Four common qualities of stress at any level of ecological organization:

1) ***Stress* is a response to or effect of an external factor (*stressor*) that is detrimental and disorganizing.**
   - **Unlike Selye's definition, does *not* include a response to or effect of a *non-detrimental* factor.**
2) **The detrimental and disorganizing factor is atypical or present at atypical levels of intensity.**
   - **Implication is that the system has not previously adjusted itself to the specific stressor to mediate its anticipated future effects.**
3) **The system responds by or is characterized by a modification in energy flow or system structure.**
   - **In the case of a response, the shift acts to reestablish or maintain some norm or homeostasis.**
   - **A return to steady-state is not essential, but is often implied.**
4) **Temporal qualities are central to the concept of stress: stress is a response to a *recent* stressor.**

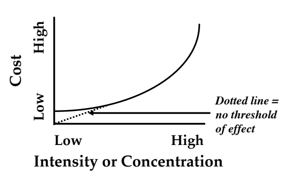
Determining Effects of Stress

Follows the 'hierarchical organization of life':

- ***Subcellular*: molecular effects and biomarkers (e.g., induction of stress proteins)**
- ***Cellular*: cytotoxicological, histopathological, and genetic effects (e.g., chromosomal fragmentation, increased aneuploidy)**
- ***Individual*: sublethal, acute, and chronic lethal effects (e.g., declines in ability to capture food or evade predators, deaths due to continued exposure)**
- ***Population*: epidemiology, population genetics, population dynamics (e.g., changes in demography)**
- ***Community* and *ecosystem* (e.g, changes in biodiversity, Photosynthesis/Respiration ratios)**
- ***Landscape*, *regional/ecoregional*, and *biosphere* (e.g., watershed pollution, changes in atmospheric chemistry)**

Types of Stress

Selyean Stress



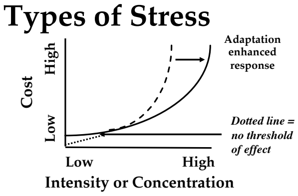
Specific or characteristic response to a recent disorganizing or detrimental factor

- **Purpose is to maintain or reestablish homeostasis (i.e., energy flow, material cycling and/or system structure) within a defined norm**
- **Not characterized by previous adaptation to the stressor**

Example: increasing pulse rate or blood pressure with exertion

Types of Stress

Preadaptive Stress



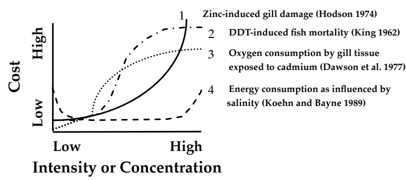
Similar to Selyean stress, *but characterized by a previous adaptation to the stressor, i.e., the system has specific information with which to mediate the effect of the stressor*

- **Adaptation may be recent and transient (e.g., acclimation) or long-term and relatively permanent (genetic adaptation)**
- **These responses tend to be specific to the stressor**

Example: induction of the P-450 monooxygenase system by polycyclic aromatic hydrocarbons (genetic response to a particular class of toxicants)

Types of Stress

Damage or Distress

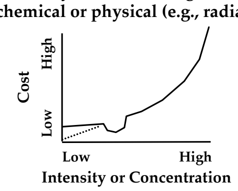


Adverse effect(s) of a stressor that are not a consequence of a system response

- **At lower levels of organization, this generally denotes cell, tissue, or organ damage**
  Examples: thinning of bird eggshells from DDT exposure. Decreased predator hunting efficiency due to intoxication

Nonstress Effects

- ***Hormesis* - a stimulatory effect resulting from exposure to low levels of some chemical or physical (e.g., radiation) agents**



Example: low concentrations of cadmium accelerated growth of wood ducks (Brisbin et al. 1987)

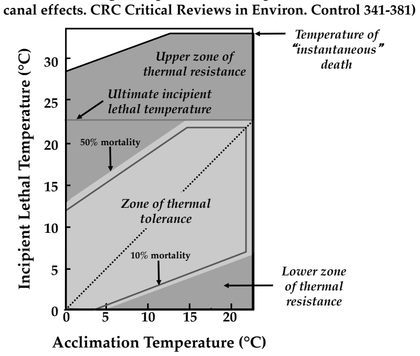
- ***Neutral effect* - measurable change that has no apparent adverse or beneficial impact on the system**
- ***Ambiguous effect* - measured effect that is undefined relative to the degree of detriment/benefit, passivity, or preadaption.** *Often seen at higher ecological levels of organization*

Stress Effects on Individuals

- ***Hormesis*: a stimulatory effect in response to exposures to low ("subinhibatory") levels of toxicants or physical agents**
  - **In ecology, this is associated with the so-called "*subsidy-stress*" hypothesis**
  - **In some animals, exposure to low-level ionizing radiation or other stressors causes an increase in lifetime reproductive output with no decrease in maternal lifespan**
  - **In humans, it forms the basis for homeopathic medicine**
- **Physiological *acclimation* and *acclimatization*: adaptive changes in an individual in response to a change in environmental conditions**
  - **More specifically, *acclimatization* refers to adaptive shifts taking place under *natural* conditions**
  - ***Acclimation* refers to shifts taking place under controlled laboratory conditions, *or* the time spent in the experimental setup before beginning measurements**

Hypothetical Thermal Tolerance in Fishes

(based on Coutant, C. 1970. Biological aspects of thermal pollution: 1. Entrainment and discharge canal effects. CRC Critical Reviews in Environ. Control 341-381)



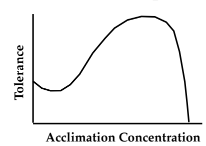
Quantifying Acclimation

Shepard (1955) quantified acclimation of speckled trout (*Salvelinus fontinalis*) to low-oxygen conditions:

- **Acclimation involved changes in the oxygen-binding capacity of blood**
- **Incipient lethal level (*ILL*, mg O_2 L^{-1}, the O_2 where 50% of the fish would live indefinitely relative to the level where 100% would die) was linearly related to the acclimation level (*A*, mg O_2 L^{-1}), such that ILL = 0.086A + 0.87**
- **Estimated the ultimate ILL (the lowest concentration to which the fish may be acclimated and still have 50% or less mortality) by solving this relationship for *ILL* = *A*:**
  $ILL = 0.87/(1 - 0.086) = 0.952$ mg O_2 L^{-1}

Quantifying Acclimation

Chapman (1985) described a general toxic response model for acclimation to metals, based primarily on LC50 data:

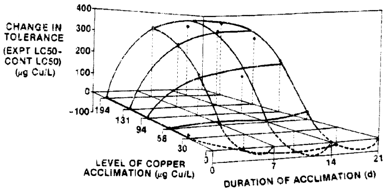


Redrawn from: Chapman, G.A. 1985. Acclimation as a factor influencing metal criteria. Pages 119-136 in R.C. Bahner and D.J. Hansen (eds). Aquatic toxicology and hazard assessment: Eighth Symposium. Philadelphia, PA, American Society for Testing and Materials.

- **As with O_2, there is a zone of roughly linearly increasing tolerance with increased acclimation concentration producing increased LC50**
  Explanation: induced response to metal that enhances tolerance
- **Maximum acclimation concentration above which tolerance decreases**
  Explanation: damaging effects exceed capacity of induced response
- **Lower limit on acclimation, below which tolerance decreases**
  Explanation: no induced response, but damaging effects still occur

Quantifying Acclimation

Dixon and Sprague (1981) change in ILL for Cu with acclimation level *and* acclimation time in rainbow trout:

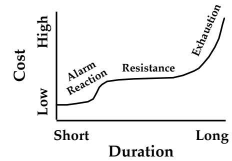


Dixon, D.G., and J.B. Sprague. 1981. Acclimation to copper by rainbow trout (*Salmo gairdneri*) – a modifying factor in toxicity. Can. J. Fish. Aquat. Sci. 38:880-888.

- **Response surface is essentially a "3-D" version of Chapman (1985) results: the "ski-jump" shape is formed by the lower limit on induced response**

General Adaptation Syndrome (GAS)

- **Also developed by Selye, consists of 3 phases:**



- ***Alarm reaction* involves immediate reactions, e.g., increased pulse rate, blood pressure, and respiration ("fight or flight" response)**
- **If stressor continues to exert effect on organism, *resistance* responses that "stimulate tissue-defense" (e.g., enlargements of the adrenal cortex, induction of metallothioneins)**
- **After a characteristic period of exposure, the organism enters an *exhaustion* phase indicating the that "finite adaptive energy" of individual has been reached. With continued exposure, the organism is unable to maintain itself and dies.**