# SECTION A

## 1. Energy flow

One of the key features of any ecological system is the capture and transformation of the energy that flows through the system. It does so only once, before it is degraded and lost as heat. Contrast this with nutrients and other resources that are capable of being recycled.

### 1.1. Energy fixation

Life can be seen as a constant flow of energy though chemical reactions to carry out the work necessary to grow, maintain and replicate its various forms. Energy comes in many forms such as heat, light, sound and electricity, and all have in common the capacity to do work. All forms of energy follow basic laws known as the Laws of Thermodynamics that determine how it can be used. The study of energy flow is important in determining limits to food supplies and the production of all biological resources.

The capture of energy and its conversion into stored chemical energy by *autotrophic* organisms (the *primary producers*) provides ecosystems with their primary energy source. Most of this is *photosynthetic*, chlorophyll-based production using light energy, and the total amount of energy converted into organic matter is the *gross primary production* (GPP); this varies significantly between ecosystems. However, plants use between 15 and 70% of GPP for their own maintenance (respiration, reproduction, etc.) and what remains is the *net primary production* (NPP) (Table 1.1.1). It is this net primary production that is available for growth and transference (through the food web) to other, *heterotrophic*, organisms. One measure of plant production is *biomass*, the total dry weight of organic matter present in a trophic level, and it is usually measured as a dry weight per unit area or volume.

***Table 1.1.1. Relative primary productivity of the major ecosystems*** (Adapted from Chiras, 1994)

| Ecosystem | Area (millions km$^2$) | Typical net primary production rate (g dry matter/m$^2$/yr) | Estimated world net primary production ($10^9$ dry tonnes/yr) |
|---|---|---|---|
| **Continental ecosystems** | | | |
| Tropical rainforest | 17.0 | 2200 | 37.4 |
| Tropical seasonal forest | 7.5 | 1600 | 12.0 |
| Temperate evergreen forest (Taiga) | 5.0 | 1300 | 6.5 |
| Temperate deciduous forest | 7.0 | 1200 | 8.4 |
| Boreal forest | 12.0 | 800 | 9.6 |
| Woodland and shrub land | 8.5 | 700 | 6.0 |
| Savannah | 15.0 | 900 | 13.5 |
| Temperate grassland | 9.0 | 600 | 5.4 |
| Tundra | 8.0 | 140 | 1.1 |
| Desert/semidesert shrub | 18 | 90 | 1.6 |
| Extreme desert, rock, sand and ice | 24.0 | 3 | 0.07 |
| Cultivated land | 14.0 | 650 | 9.1 |
| **Total terrestrial** | 145 | 742 | 110.5 |
| **Aquatic ecosystems** | | | |
| Swamp and marsh | 2.0 | 2000 | 4.0 |
| Lake and stream | 2.0 | 250 | 0.5 |
| Open ocean | 332.0 | 125 | 41.5 |
| Upwelling zones | 0.4 | 500 | 0.2 |
| Continental shelf | 26.6 | 360 | 9.6 |
| Algal beds and reefs | 0.6 | 2500 | 1.6 |
| Estuaries and brackish waters | 1.4 | 1500 | 2.1 |
| **Total marine** | 365.0 | 163 | 59.5 |
| *Total biosphere* | 510 | 333 | 170 |

## 1.2. Energy flow

Having been captured and converted by autotrophs, the energy then flows through the ecosystem according to the Laws of Thermodynamics.

### *Box 1.2.1. The laws of thermodynamics and matter transformations*

The *first law* (the law of conservation of energy) states that in a closed system, energy can neither be created nor destroyed but can only be transformed from one form to another. The key point, therefore, is that in any such system the total amount of energy consumed will equal the total amounts being produced in all its various other forms. Photosynthetic organisms capture and transform light energy from the sun and this energy is transferred throughout the ecosystem, subject only to the consequences of the second law.

The *second law* states that disorder (entropy) in the universe is constantly increasing. This means that during energy transformations, energy is inevitably degraded to less organised and useful forms; the least useful form and principal loss upon any transformation is heat.

Strictly speaking, energy does not circulate since it enters the system only once and as it flows through the system, it is gradually degraded to heat which is the least useful form. Energy flow, therefore, is the movement of energy through a system from an external source, through a series of organisms and back to the environment as degraded energy.

Figure 1.2.1 shows the way energy flows through the various layers of the ecosystem. Each layer is referred to as a *trophic* (feeding) *level* and from it a significant proportion of energy is lost as metabolic heat and a further proportion is waste or uneaten material that passes to the *decomposer* level. What is left is available to the next trophic level. Studies have shown that at each stage in this transfer only a small fraction, rarely exceeding 10% (the *trophic efficiency*), of the available energy is actually available to the next level. This low conversion efficiency is due largely (Figure 1.2.2) to:

- not all material at any trophic level being consumed
- not all material ingested being digested, much passing through the digestive system as roughage
- most of the material digested being used for catabolic processes to provide the organism with its energy requirements.

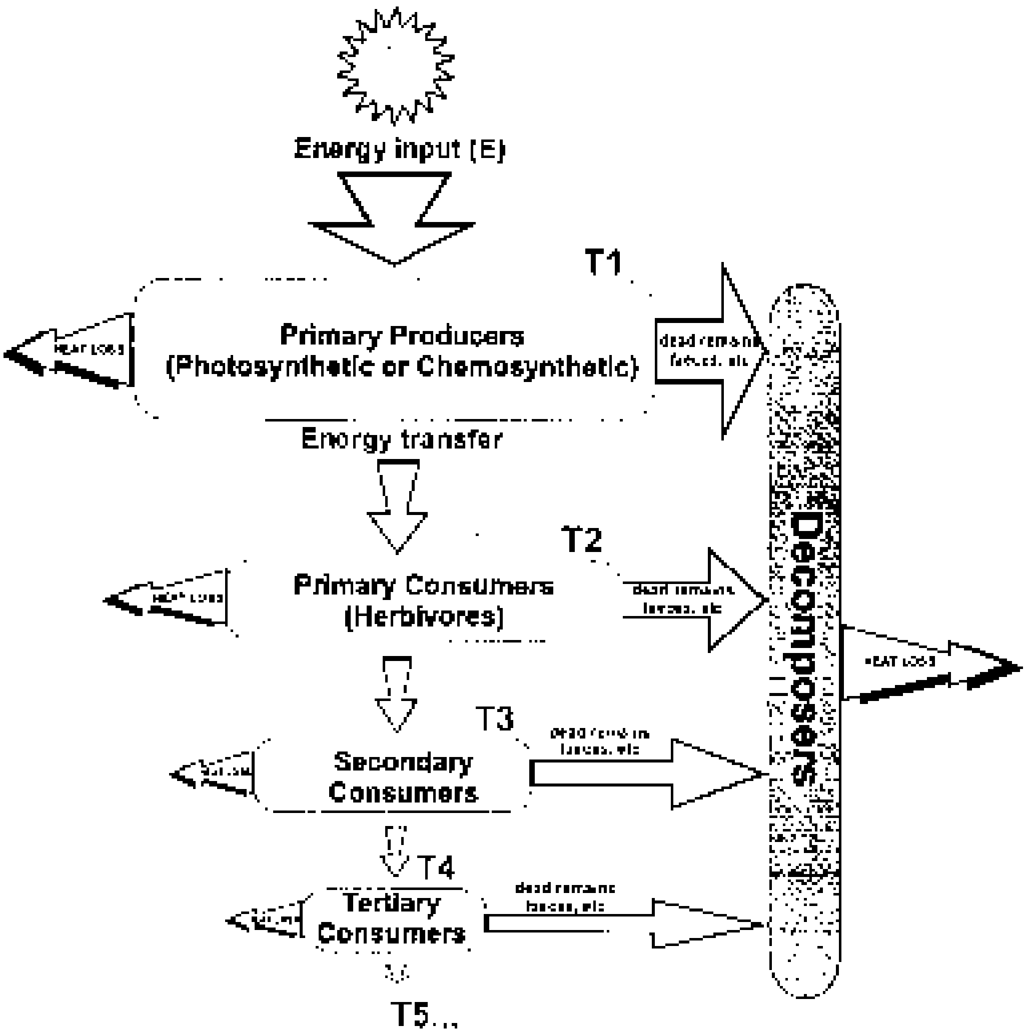

***Figure 1.2.1**: Energy transfer and flow through a simple hypothetical ecosystem. The area of each box is proportional to the biomass at that level.*

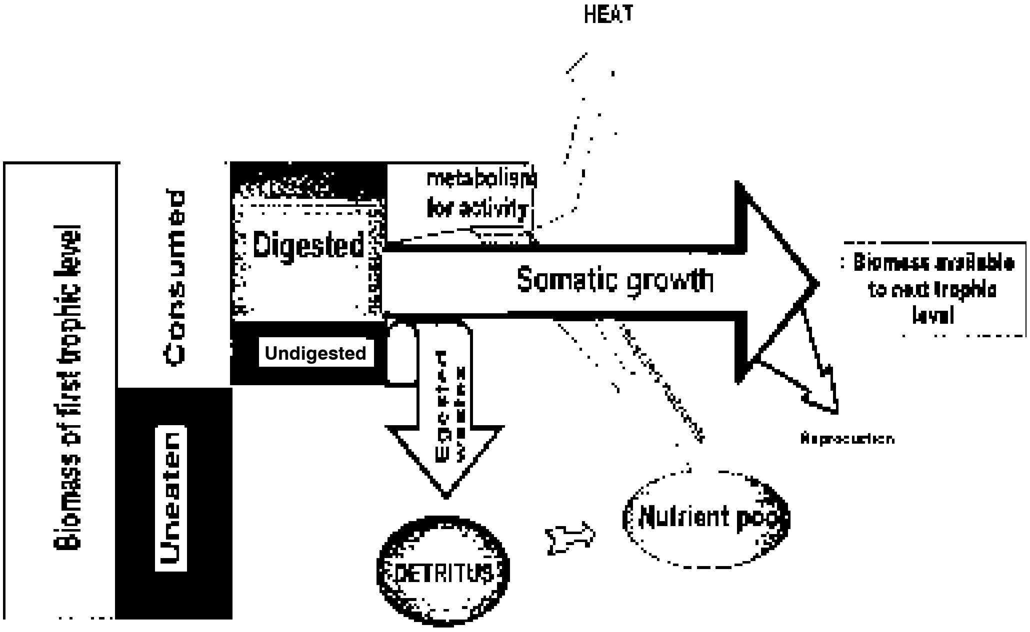

*Figure 1.2.2: A summary of the ways in which energy is lost during trophic level transfers.*

This '*ten per cent rule*' is particularly important since it places limits on the potential number of trophic levels in a system, few systems supporting more than four or five trophic levels. This is because the energy available to the higher trophic levels is rarely sufficient to support large numbers of consumers (for example, 1000 tonnes of primary producer can support only 0.1 tonne of a trophic level 5 (T5) consumer).

Elton (1927) introduced the concept of the *pyramid of numbers* (Figure 1.2.3) to demonstrate this principle, but it does not always work. For example, when parasites are involved or the primary producer comprises one large organism (such as a tree), the pyramid may become partially inverted. *Pyramids of biomass* are, therefore, often used instead. These are more reliable but where rates of primary production are high, such as in phytoplankton communities (see Figure 1.2.4), they too fail to retain the expected structure because the measure of standing crop represented by the biomass pyramid fails to take rates of primary production into account. The very high rate of primary production is able to support a larger biomass of secondary producers than would normally be possible. The only reliable form of model is a *pyramid of energy flow* or *productivity* (Figure 1.2.5).

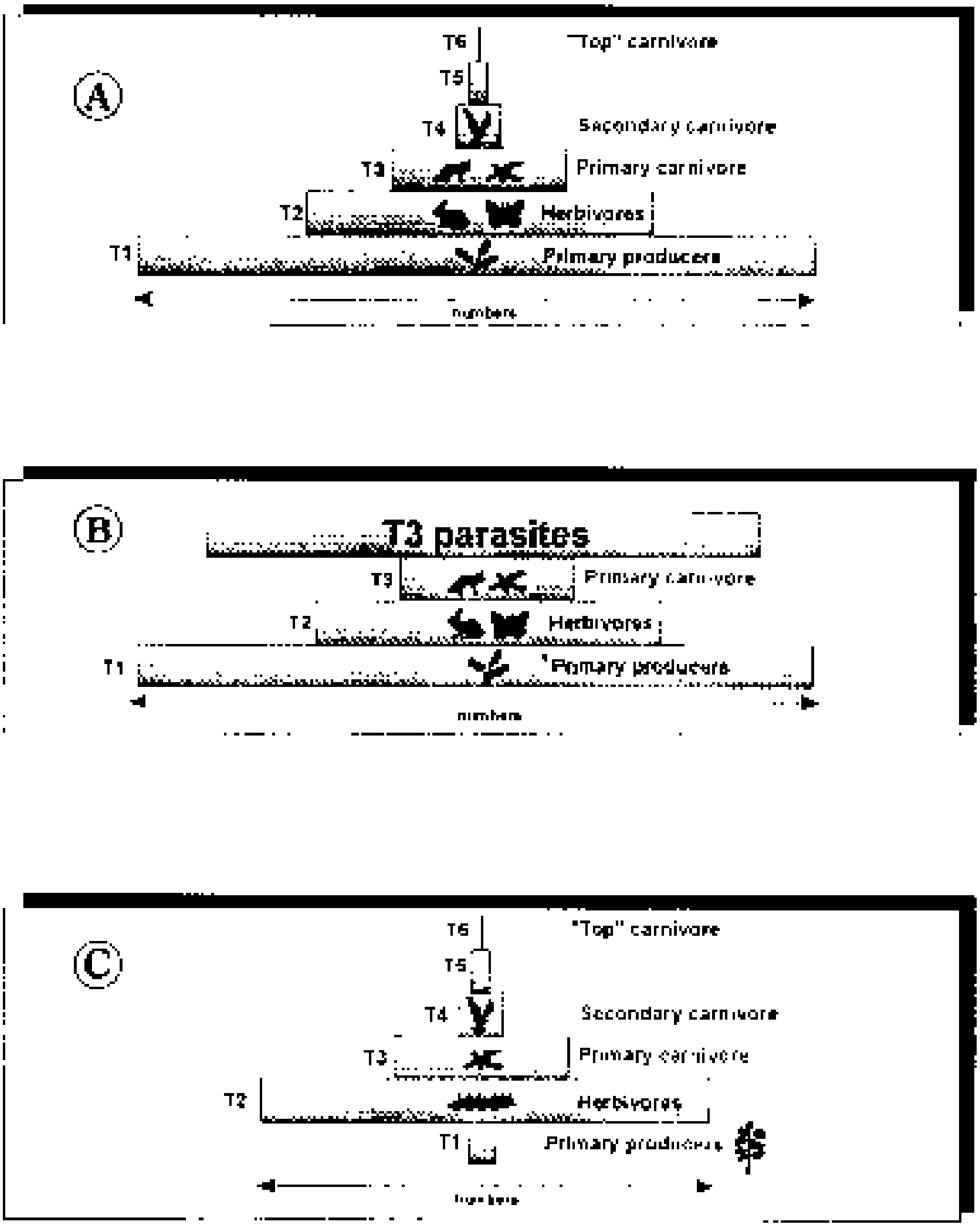

***Figure 1.2.3**: Examples of pyramids of numbers.*

*A. The typical theoretical pyramid showing a steady decline in abundance with increasing trophic level.*

*B. The inverted pyramid associated with a parasitic trophic level.*

*C. The pyramid associated with the occupation of a large food resource such as a tree where the abundance of the primary producer obscures its supporting role (in primary production terms).*

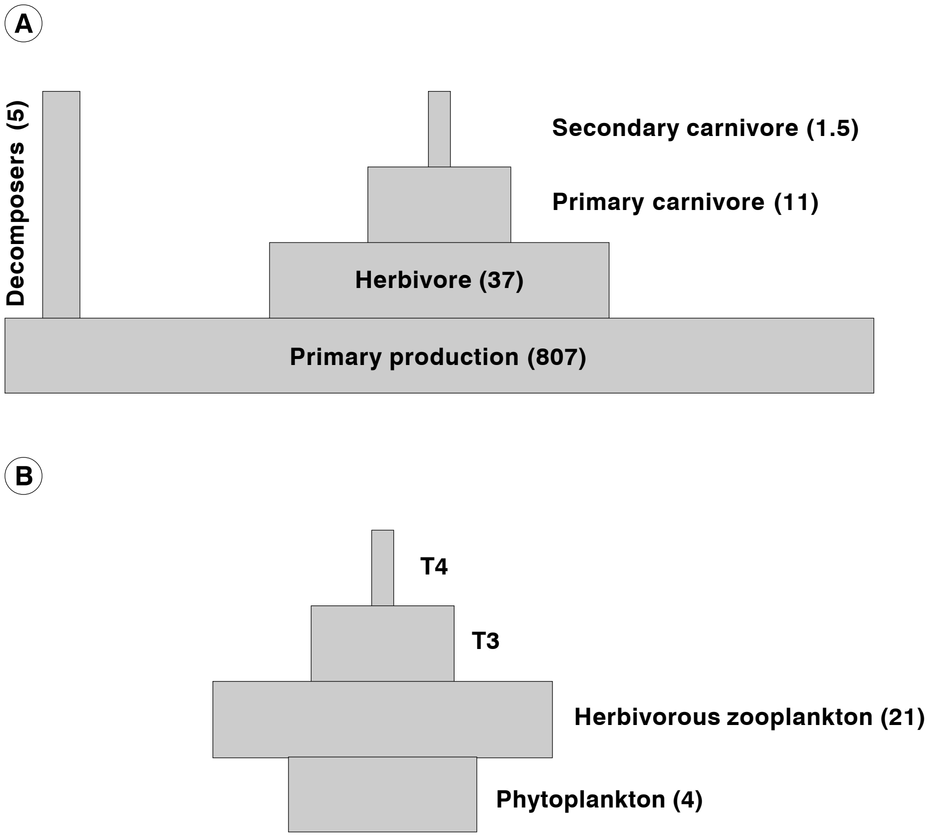

***Figure 1.2.4****: Pyramids of biomass in which all quoted values are in g per sq. m. A. The expected pyramid resulting from the 10 per cent rule. B. The inverted pyramid typical of marine planktonic food webs. This occurs because the extremely high production rates of the phytoplankton enable a relatively small standing crop to support a much larger biomass of zooplankton.*

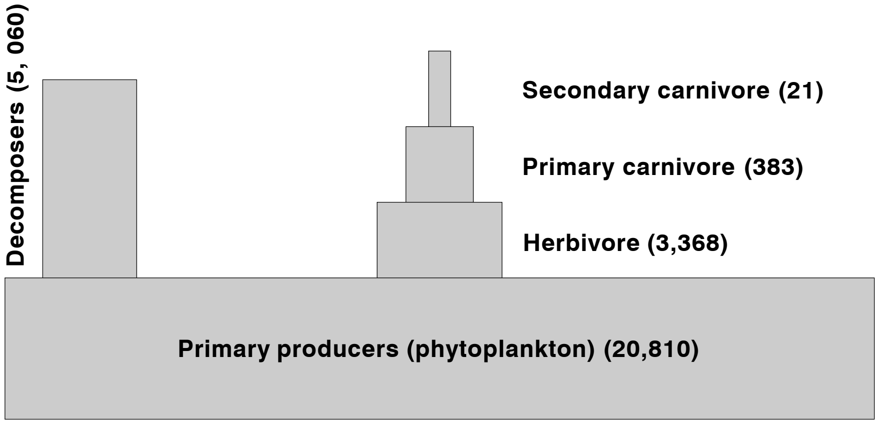

***Figure 1.2.5****: Pyramid of energy flow for an aquatic system in Silver Springs, Florida. Values are kcal per sq. m per year (adapted from Miller 1994).*

The linear passage of energy along classical *food chains* is rare in nature and most consumers are usually part of a *food web* system. True food chains such as used by the blue whale (phytoplankton > krill > blue whale) represent risky strategies because each link is dependent upon the one below. A web on the other hand provides relative stability since it allows the utilisation of *substitutable resources* at any level. Figure 1.2.6 shows how two closely related herring species have adopted quite different strategies. Some webs are extremely complex but the number of trophic levels in any one pathway remains restricted by the ten per cent rule.

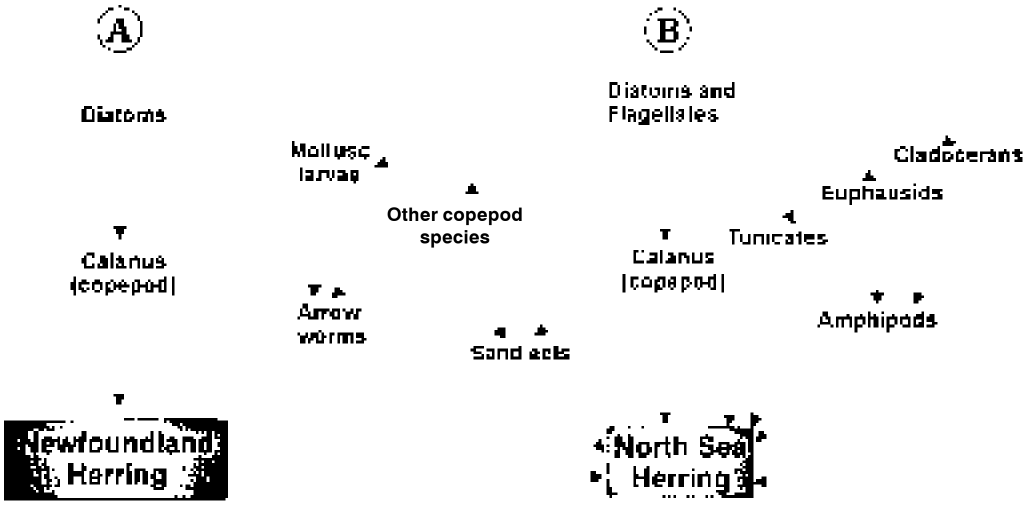

***Figure 1.2.6**: A comparison of a food chain (A) with a food web (B) for related species of Herring. The Newfoundland Herring feeds on a particular species of copepod while the North Sea Herring has substitutable food resources.*

The ecological importance of *decomposers* is almost as significant as that of the primary producers. They degrade detritus and waste materials, releasing nutrients and other materials for recycling. Decomposers are largely aerobic species, requiring oxygen to degrade the organic materials and aeration is an important variable in the control of decomposition. Decomposition activity, therefore, can also result in depletion of oxygen levels in organically loaded systems. Without the decomposition process, the primary and secondary producers would soon become limited by resource shortages, and the remains of primary and secondary producers would accumulate thus tying up the nutrients and other resources present in the bodies of the dead organisms. The decomposers are themselves the basis for food webs and thus provide energy to a further series of organisms before the energy is finally degraded to heat.

## 2. Circulation of nutrients

Materials necessary for the maintenance of ecological systems are recycled subject to a variety of environmental constraints and timescales. These can be described as *biogeochemical cycles* since the cycling involves both biotic and abiotic processes.

### 2.1 Decomposition

Decomposition is the gradual breakdown of dead organic matter and involves a combination of both physical and biological processes. It results in the release of inorganic nutrients that become available for uptake by plants and other primary producers. The organic matter in soil is composed of litter (dead plant material), droppings (animal waste) and the dead remains of plants, animals and microbes. Two main groups of organisms are involved: *detritivores*, detritus-eating invertebrates from a wide range of taxonomic groups, and microbial *decomposers* (mainly bacteria and fungi).

Decomposers comprise the microbiota capable of breaking down the complex structural molecules of organic debris, particularly abundant and tough molecules such as cellulose and chitin. The result of this, usually external enzymatic digestion, is the production of simpler breakdown products that can be metabolised (respired) by the microorganism. The rate of decomposition is increased by the taxonomically diverse, detritus-feeding invertebrates comprising the detritivores. They are typical consumers in that they feed on detritus to obtain nutrients and energy, but their main contribution is the physical reduction of detritus particle sizes to produce *humus*, the partly decayed organic portion of soil that forms a vital component of productive soil. It also serves to increase the surface area for the decomposers to work on, both inside the organism's gut and externally. In the absence of detritivores, the rate of microbial decomposition is reduced.

The rate of decomposition varies in space and time and is influenced by a number of factors including:

- the type of detritus (for example, deciduous leaf litter decays more easily than coniferous litter)
- the type and abundance of decomposer organisms present
- environmental conditions such as temperature, moisture, aeration and nutrient availability.

The net result of these processes is the release of nutrients and minerals previously locked away in the bodies of dead organisms, a process termed ***mineralisation.*** Figure 2.1.1 summarises the processes involved. Available nitrogen, however, can often become limiting in terrestrial soils because its release by natural decomposition can be relatively slow. Hence nitrogen fertilisers are frequently applied to soils and composts to circumvent this slow release (see next section).

Remember, all organisms are ultimately subject to the decomposition process, which therefore comprises the final trophic level, extracting the maximum amount of energy from the system and recycling materials.

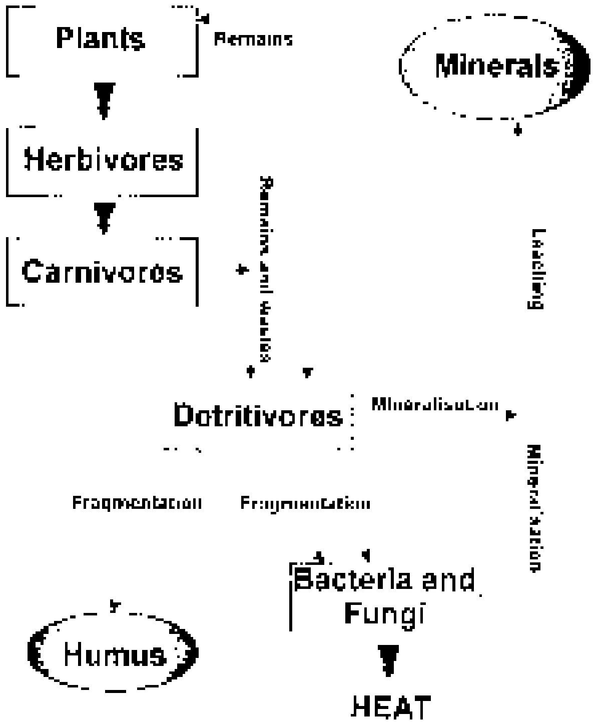

***Figure 2.1.1****: A summary of the role of decomposers (detritivores and bacteria/fungi) in an ecosystem.*

## 2.2 Nutrient cycling

All organisms require a complex array of basic minerals (nutrients) to function physiologically. Animals obtain such materials mainly from their food, whilst plants and microbial species absorb them from the environment. Nutrients are divided into the macronutrients such as nitrogen, phosphorus and sulphur (required in relatively large quantities) and micronutrients (trace elements) required only in very small quantities. Minerals must be in a soluble form to be absorbed, whether from the environment or from the alimentary system, and there is a close relationship between water and minerals as resources. Lack of water can result in nutrients being unavailable. Soils and waters may differ markedly in their mineral status.

All nutrients move around within *biogeochemical cycles* where they may:

- become fixed into a biotic or abiotic component
- be taken up or lost as a result of absorption or leaching
- be chemically transformed by biological or environmental processes.

This unit focuses on two aspects of nutrient cycling, specifically the nitrogen cycle and the phosphorus cycle.

**Nitrogen** is an abundant, chemically inert gas making up some 80% of the Earth's atmosphere. This gaseous form is very stable and has to be transformed into biologically useful forms before it can be used by most organisms. There are a number of biologically useful oxygenation states and biologically mediated redox reactions are central to the nitrogen cycle. The nitrogen cycle (Figure 2.2.1) contains five main biologically mediated steps, all heavily dependent upon microbial activity and with soil systems representing an important sub-system within the larger nitrogen cycle. These five steps are listed below.

1. *Biological nitrogen fixation*, the biological conversion of gaseous nitrogen to ammonia. This requires the enzyme *nitrogenase*, which only works in the absence of oxygen, and the input of large amounts of energy. Only a few species of prokaryotic bacteria and cyanobacteria are involved, and these may be either free-living or in symbiotic association with plants, as in the root nodules of legumes.

2. *Nitrification*, the conversion of ammonia to nitrate by soil bacteria. This involves two groups of bacteria: *Nitrosomonas* and *Nitrococcus* species convert ammonia to nitrite; *Nitrobacter* then oxidises nitrite to nitrate, releasing energy in the process.

3. *Assimilation*, the uptake of nitrate and/or ammonia by primary producers and their incorporation into proteins or nucleic acids. These materials then pass along the food chain through digestion and assimilation at each trophic level.

4. *Ammonification*, the decomposition of the nitrogen-containing dead organisms and animal wastes to ammonia by bacteria in soil and aquatic systems. This ammonia is recycled and is available to steps 2 and 3.

5. *Denitrification*, the reduction of useful nitrate to unusable gaseous nitrogen. This represents a continuous loss of useful nitrogen from the system. This relatively limited process is carried out by anaerobic denitrifying bacteria.

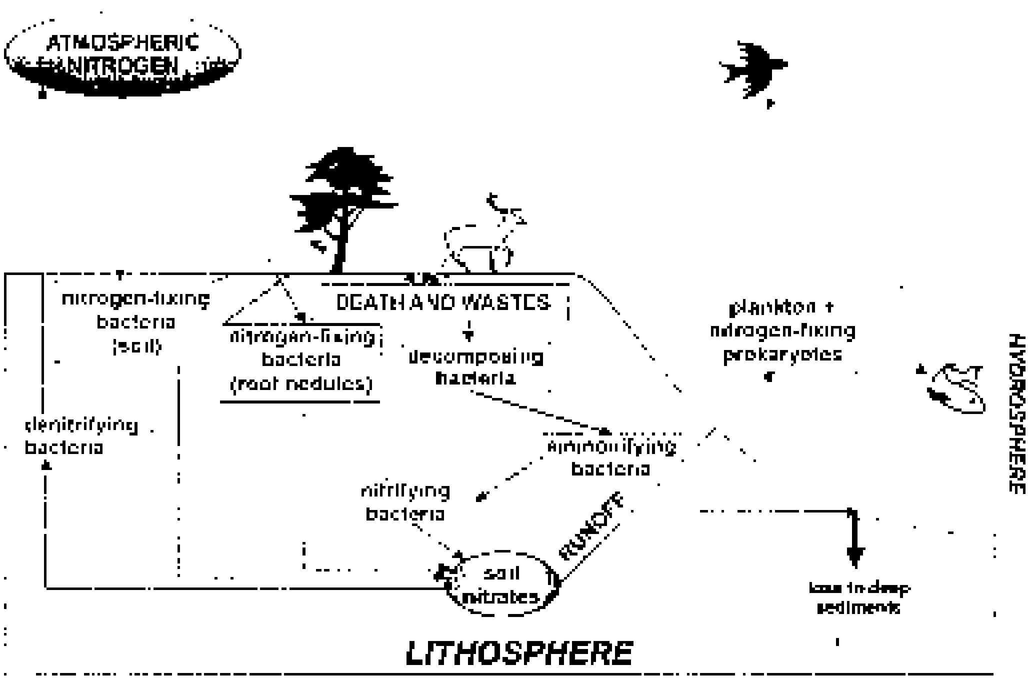

***Figure 2.2.1****: The nitrogen cycle.*

Remember that not all nitrified nitrogen is subsequently taken up by plants since some of the highly soluble nitrate is leached from the soil by percolating water and ends up in the oceans. Denitrification is also known to occur chemically in aerated soils. Habitat characteristics such as water saturation (for example, flooding) and resultant anaerobic conditions may have important influences on the flux of nitrogen. Nitrogen, therefore, despite its atmospheric abundance, can be limiting and can be in short supply in particular habitats and at particular times. The use of crop rotations that include nitrogen-fixing leguminous species and/or the use of nitrogen fertilisers for intensive agriculture are responses to such potential shortages.

**Phosphorus** plays a central role in cell metabolism and reproduction and is a key constituent of energy-transferring molecules (ATP, ADP and AMP) and the nucleic acids, DNA and RNA. However, naturally occurring phosphorus minerals are relatively insoluble and have very low volatility, there being no gaseous forms. The phosphorus cycle (Figure 2.2.2), therefore, has its primary reservoir in sedimentary rocks from which phosphorus is weathered, largely in particulate form. The low solubility of its compounds results in relatively little phosphorus being present in solution (the biologically available form usually being phosphate) in soils or aquatic systems and virtually none in the atmosphere. Phosphate fluxes, therefore, result largely from the movement of solid particles in air and water or the transfer within and between organisms through trophic interactions. Much of the phosphorus store (particulates) in soils and sediments is biologically unavailable. Even in systems where it is relatively abundant, the low concentrations in solution may limit growth. This is particularly important for the nitrogen fixers, where nitrogen is never limiting. The addition of soluble phosphates as fertiliser has become common in the cultivation of crops, especially legumes, although these are readily precipitated within the soil system (phosphate fixation), where the pH is very important in soil-inorganic phosphate interactions. In general, phosphorus cycles much more rapidly through marine organisms than through terrestrial ones.

Human activity has significantly increased the phosphate levels in the environment. Inland waters receive phosphorus from leached fertilisers and from the addition of phosphate-based water softeners to detergents. This can lead to algal blooms, which produce water stagnation problems or, in the case of cyanobacterial blooms, direct toxicity.

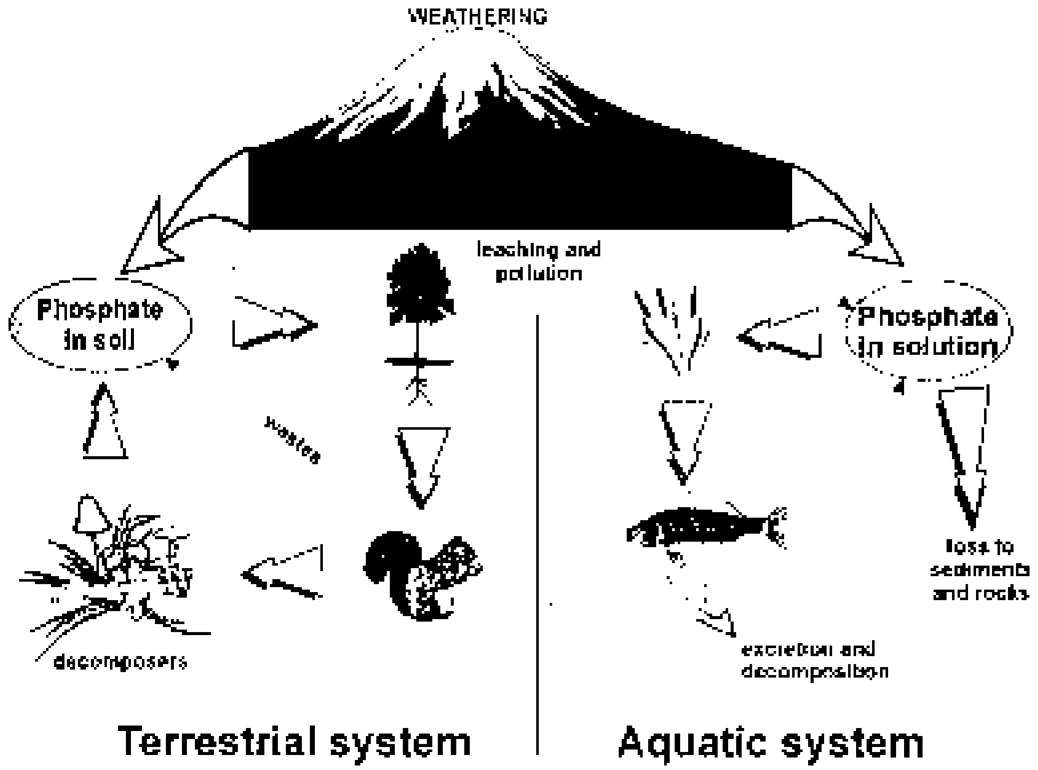

*Figure 2.2.2: The phosphorus cycle.*

## 3. Biotic interactions

Organisms interact with all abiotic and biotic components of their environments. The abiotic components are the *conditions* and non-living *resources* that characterise their particular habitats and these must remain within the normal physiological and behavioural tolerances of the organism/species for survival, growth and reproduction. However, organisms live within a complex matrix of other organisms of both their own and other species. Interactions between members of the same species are termed *intraspecific* and those between species *interspecific*. The latter can be very strong selection factors in evolution and may result in coevolution between two species. Biotic interactions fall into two broad categories: *competition*, where both species may suffer as a result of interaction, usually for a limited resource, and *predation* (which includes *grazing*), where one species consumes another, benefiting one species only. These categories are, of course, intimately related: for example, predators are frequently in competition with each other for a particular food resource.

### 3.1 Predation

Predator–prey interactions, effectively the interactions between food resources and their consumers, exert very powerful controls on populations and their evolution. Types of predators include diverse categorisations, for example herbivores (mainly as grazers), carnivores, parasites and filter feeders.

The basics of predator–prey interactions are now well established and are frequently cyclic in nature. The predators consume prey and increase in numbers until the prey density is reduced to below a threshold. The predators are then subject to starvation and their numbers fall. The pressure on the prey species is then reduced allowing them to increase again, and so the cycle repeats (Figure 3.1.1). Theoretically, a stable balance between predator and prey densities should result, but the other diverse factors affecting population densities (for example reproductive rates, death and disease rates and environmental conditions) always tend to act against such stability developing. There is much debate about the significance of predator–prey relationships which vary considerably between different species and environments. However, population cycles are characteristic of some species of small mammals, such as lemmings, and sometimes these are clearly related to predator abundance. Similarly, plagues of rodents in some countries, for example India, are attributed to the reduction in the predatory snake populations by humans.

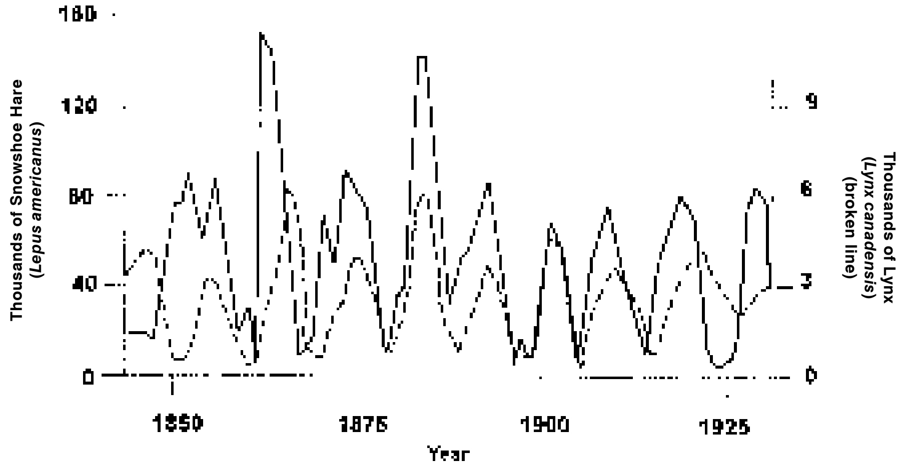

***Figure 3.1.1****: Oscillations of a predator (Lynx) – prey (Snowshoe Hare) system in Canada, based upon long-term data from the Hudson's Bay Company.*

The dynamics of predator–prey interactions forms the basis for the development of biological control methods, where the optimal situation is to introduce a predator that reduces, but does not eliminate, the prey (pest) species.

The complex interactions between predators and their prey are also important for the maintenance of diversity in ecosystems. This is because, by controlling the relative abundance and distribution of some species, opportunities are provided for other species by reducing or preventing the competitive exclusion of less competitive forms. The interactions also facilitate long-term evolutionary change, since prey species tend to evolve a rich variety of responses to predation, which result in them becoming more difficult to eat. This includes the development of spines, hairs and bristles, toxic or noxious chemicals, mimicry and behavioural defence mechanisms. In their turn, predators also evolve to become more effective in overcoming such defences. This is one form of co-evolution.

Morphological defences against predation mainly comprise methods of hiding (*crypsis*) or of adopting warning coloration. Crypsis is exhibited by animals such as stick insects, many caterpillars and transparent aquatic species. Such animals may be palatable, but their cryptic shapes and colours reduce the risk of predation. Warning coloration (*aposematism*) is the adoption of bright colours (usually red) and patterns (for example yellow and black stripes) by noxious or dangerous animals, effectively advertising their dangerous nature. The yellow and black coloration of bees and wasps warns of their stinging capability. The effectiveness of such defences is shown by two forms of *mimicry* that make use of such warnings for the protection of harmless, palatable species. In Batesian mimicry the species mimics in both appearance and behaviour an unpalatable or harmful organism, for example many of the butterflies and moths. For this to be successful the model must outnumber the mimic. In Mullerian mimicry several unrelated but unpalatable, aposematically coloured species come to resemble each other, effectively reinforcing the message. Thus, different kinds of stinging wasps have yellow and black striped abdomens despite not all being descended from a yellow and black striped ancestor.

### 3.2 Grazing

Grazers attack large numbers of prey (plant or animal) but they may remove only a part (for example a shoot or limb) of each prey item. Their impact is, therefore, damaging but not lethal, usually allowing re-growth to occur. This is particularly true for modular prey items such as plants and corals, where modules can be replaced. The effects of grazing may be highly significant in the control of species diversity and the impact of grazing on vegetation may change community structure. This is because those plant species with basal meristems, such as the grasses, can be safely grazed without suffering mortality. Those without such protected meristems can be eliminated by grazing when the entire aerial component is removed.

### 3.3 Competition

Competition between individuals (intraspecific) or species (interspecific) is most intense for resources such as space, food and water and is a potent force in structuring communities. Competition increases with density, or with reduction in the quantity of the resource, or both, but will be significant if the resource becomes limiting. When the consumer significantly reduces the resource, *exploitation competition* results, for example in human fisheries. When one species prevents other individuals from using a resource, it is called *interference competition*. The negative effects of competition result in features such as reduced growth or reproduction rates, exclusion from a habitat or increased mortality. Intraspecific competition may be severe because individuals have similar requirements in all respects and, therefore, compete directly.

Competitive interactions may be very complex, leading to short-term variations in abundance and distribution, and to long-term evolutionary adaptations to provide improved competitive ability within its particular niche.

A *niche* (Elton, 1927) is a multi-dimensional concept of the unique position occupied by a particular species within a community, comprising the physical, chemical, biological, spatial and temporal factors required for the survival of that species. It therefore represents the sum of:

- an organism's adaptations
- the resources it needs
- the lifestyle to which it is fitted.

Niches may be divided into two types. The *fundamental niche* is the theoretical, multi-dimensional niche that would be occupied in the absence of other species, while the *realised niche* is the actual niche occupied in a community where there are competitive interactions and consequent sharing of resources with other species. The key rules are that:

- no two species may occupy *exactly* the same multidimensional niche in the same community for any length of time because competitive exclusion of one of the species will occur; one species will eliminate its competitor
- fundamental niches can *overlap*, a feature common in nature, leading to competitive co-existence. It is this competition that defines a species' realised niche.

A useful exercise is to research the knowledge relating to fundamental and realised niches for common species, for example garden birds or small mammals. The consequence of overlapping niches and the resulting competition for resources is the development of *resource partitioning* – the dividing up of the use of each resource by species specialisation and adaptation. This allows the exploitation of different components of the resource by different organisms and is well illustrated by the specialisation of beaks in birds (see Figure 3.3.1) and in the grazing of large herbivorous mammals in the Serengeti Plain in Tanzania.

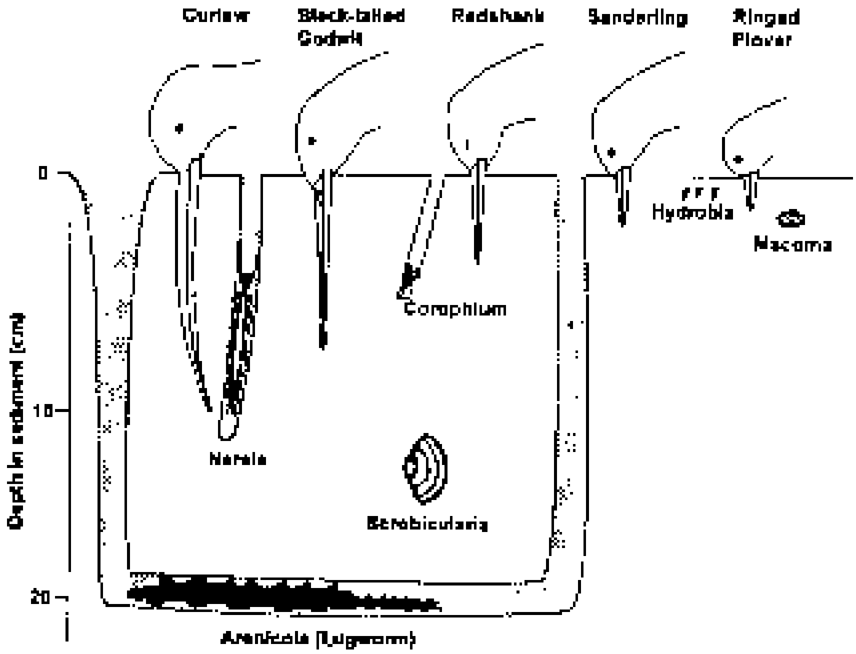

***Figure 3.3.1**: Diagram showing how the differing lengths of the beaks of estuarine wading birds facilitate the utilisation of different food species (resource partitioning). Modified from Green (1968).*

The significance of competition becomes conspicuously visible when species have been introduced, accidentally or intentionally, into new communities by human activity. The introduced species (also known as alien or exotic species), frequently out-compete indigenous species and so alter community structure. Excellent examples, easily developed into literature research activities, include the introduction of rabbits to Australia, zebra mussels in the United States, *Sargassum muticum* to the United Kingdom or Africanised bees to South America. A major factor in the success of such introduced species is the frequent lack of controlling predatory species in the country of introduction, allowing such species to grow out of control. If the introduced species occupies the same niche as an indigenous species, it often results in the elimination, or at least severe reduction, of the native organism.

Most communities contain a variety of species with niches that overlap to varying degrees. This allows the survival of some weaker competitors, albeit in reduced numbers, providing the raw material of diversity and facilitating the potential for change in community structure when and if conditions change. Such changes are typical of successional sequences and recovery from natural disasters. Patchy environments also provide a patchwork of local conditions that favour the survival of different species, each patch thus acting as a reservoir of diversity.

# 4. Symbiotic relationships

Symbiosis ('living together') is a term that includes a variety of interactions in which two species, the host and its symbiont, maintain a close relationship. The importance of symbiotic relationships has become much more widely appreciated in recent decades as the widespread role of mutualistic relationships has become evident (for example in coral reefs). As with predation, co-evolution occurs and the species become closely adapted to each other. Three types of relationship are recognised, depending on the nature of the relationship.

## 4.1 Parasitism

Parasitism is a relationship that is beneficial to one species (the parasite) but is frequently damaging for the host species. The parasite exploits the host by living in or on the host and derives its nutrition from the host. However, the most effective parasites are those that do not cause the host to die, at least until the parasite's life cycle is complete. There is always a balance between parasitic damage and host defence mechanisms, which can result in the evolution of a relatively stable relationship. Parasites may be:

- *ectoparasites* such as ticks, fleas and leeches, which remain external to the host or
- *endoparasites* such as tapeworms, liver flukes and malarial parasites which live within the body of the host.

Most parasites are *obligate*, that is they must live parasitically. Some fungi are *facultative* parasites since they can become saprotrophic once their host has died. Many parasites have a complex life cycle and may use a secondary host or hosts for dispersal or completion of the stages of development (Figure 4.4.1). Parasites are transmitted to new hosts by a variety of mechanisms including:

- direct contact
- production of resistant stages that are released to the environment and that hatch when eaten by a host
- use of other secondary host species (vectors) to transmit and develop infectious stages; for example the mosquito is the vector for *Plasmodium* (malaria).

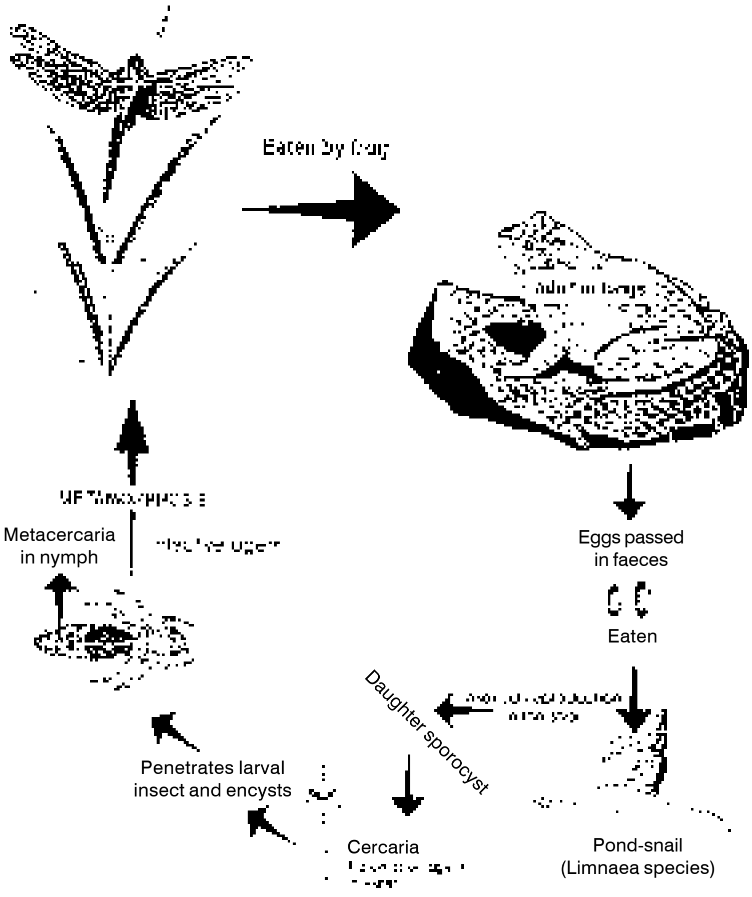

*Figure 4.4.1: The complex life cycle of* Haematoloechus variegatus, *a digenean parasite of amphibian lungs.*

Most host–parasite relationships are fairly species-specific as a result of the co-evolution of parasite and host. The development of a parasitic infestation is countered by host (immune) reactions to which the parasite then further adapts. This cyclical evolutionary war tends to result in increasing host specificity the longer the relationship has existed.

## 4.2 Commensalism

Commensalism is the name given to a relationship that is beneficial only to one (the commensal) of a regularly occurring pairing of species, the partner being unaffected by the relationship. Few examples of strict commensal relationships exist because it is unlikely that one partner in an ecological interaction will ever be unaffected by the other. The typical examples quoted are hitchhiking species, such as anemones living on crab shells, but there will be energetic consequences for the host as well as feeding benefits for the commensal. Most of the examples given in the literature relate to feeding relationships or to the provision of protection.

## 4.3 Mutualism

Mutualism is characterised by both members of a relationship receiving benefit from that relationship and such relationships require the evolution of adaptations in both participating species. Many co-evolved mutualistic relationships have been discovered and this type of relationship is now known to be remarkably common and vital to many forms of life. Such relationships are known to occur between:

- plants and micro-organisms; for example leguminous plants such as peas and beans which protect and encourage the growth of nitrogen-fixing bacteria (*Rhizobium* species) in their root nodules in return for receiving usable nitrogen compounds
- protists and fungi in the form of compound organisms called lichens and in mycorrhizas. Lichens contain modified fungi in association with either cyanobacteria or green algae. The fungi provide the support, water and nutrients while the micro-organisms photosynthesise and provide chemical products to the fungus
- terrestrial plants and insects, intimately related through often highly specialised pollination mechanisms, for example orchids. *Acacia cornigera* plants provide special facilities for a particular genus of ants (*Pseudomyrmex*), which in return protect the tree from many leaf-eating insects and other herbivorous species
- animals and protists, which have extremely important associations. Herbivores such as termites and ruminants use gut bacteria to enable them to digest cellulose. Corals and giant clams culture algae within and between their cells, providing the algae with protection and nutrients in return for photosynthetic products
- animals and other animals; for example some ants culture and raise aphids in return for sweet secretions produced during aphid feeding. Cleaner fish and shrimps remove ectoparasites (as food) from their customers, whose inaccessible regions are thus protected from parasites.

The evolution of mutualisms involves the development of intimately connected structures, behaviours, physiologies and biochemistries. These frequently involve an exchange of metabolites to support the relationship. Some of the most important mutualisms occur between different kingdoms and are of great ecological importance; for example coral reefs are founded upon the relationship between the coral and their unicellular algae.

# 5. Costs, benefits and consequences of interactions

Species and individual interactions can be broadly considered as trophic interactions and competitive interactions, as described in other sections. Clearly such interactions have consequences for ecosystem energetics, dynamics and productivity.

## 5.1 Interaction between species

The interactions between individuals of a species or populations of different species may have positive, negative or neutral effects as summarised below.

***Table 5.1.1. Summary of types of interaction***

| *Interaction* | *Effects on population density* |
|---|---|
| Predation | Beneficial to one species (predator) and detrimental to the other (prey) |
| Parasitism | Beneficial to one species (parasite) and detrimental to the other (host) |
| Commensalism | One species benefits (the commensal) while the other is largely unaffected |
| Mutualism | The interaction is beneficial to both species |
| Competition | The interaction is detrimental to both organisms |

The delicate balance that is the consequence of most symbiotic relationships is affected by both biotic (host health) and external factors (environmental conditions). In parasitic relationships, healthy hosts may be able to tolerate a parasite's presence, whilst already stressed hosts (stressed either by other infections or environmental conditions) may succumb rapidly to a parasitic infection. Compare the mortality rates for diseases in developing countries with those in the western world to provide evidence for this effect. Host health, be it plant or animal, can be influenced and managed by the use of pesticides or drugs that alter the balance of the parasitic relationship in favour of the host species.

A good example of the influence of environmental conditions is seen in the problem of coral bleaching. Here rising sea temperatures, perhaps attributable to global warming patterns, appear to be causing the loss of the unicellular symbiotic zooxanthellae from coral species, most of which are now known to require this mutualistic relationship for survival. This requires only a relatively small increase in sea temperature and once the zooxanthellae have been driven out, the coral dies and turns white – hence the term coral bleaching.

The maintenance and impact of symbiotic relationships is, therefore, very susceptible to the impact of both internal and external factors. An understanding of such relationships facilitates our control of changes to promote human, animal and plant health by the management of the quality of the host environment. An example relating to the maintenance of nitrogen levels in soils through good practice is given in Box 5.1.1.

### *Box 5.1.1. Nitrogen fixation and root nodules*

Important symbioses, such as that associated with nitrogen fixation in root nodules of leguminous species, are vital and can be fostered by appropriate land management practice. For many plants, the scarcity of usable nitrogen compounds in the environment is one of the main growth-limiting factors. Gaseous nitrogen is abundant (78 per cent of the atmosphere) but unavailable. Although conversion of gaseous nitrogen to a usable form is carried out by a few groups of prokaryotic (kingdom *Eubacteria*) organisms, it requires a great deal of energy to do so. This process of nitrogen fixation reduces gaseous nitrogen to ammonia using an enzyme called *nitrogenase* and frequently the nitrogen fixers live in intimate association with a specific eukaryotic organism. Their role in the biosphere is just as important as that of the photosynthetic autotrophs, although their biomass is relatively small. They fix some ninety million tons of gaseous nitrogen per year, by far the most significant source of world nitrogen fixation. Various photosynthetic bacteria, including cyanobacteria, are the main nitrogen fixers. On land, free-living soil bacteria make only a relatively small contribution to terrestrial nitrogen fixation, most of it coming from the bacteria associated with the formation of root nodules in certain plants.

Some bacteria belonging to the genus *Rhizobium* live in close association (mutualistic symbiosis) with the roots of leguminous seed plants such as peas, soybeans, alfalfa and a variety of tropical shrubs and trees. These nodule bacteria release up to 90 per cent of the nitrogen they fix to the plant and also excrete some amino acids into the soil, making some nitrogen available to other organisms. By this means, nitrogen-poor soils can both be cultivated and improved, and for this reason crop rotations usually involve the periodic growing of leguminous plants to help improve the soil.

The formation of nodules results from free-living *Rhizobium* bacteria interacting with the growth of root hairs. A nodule forms as the plant's reaction to the initial infection by the bacterium and the bacteria then multiply, rapidly filling the host cells with bacteria (*bacteroids*). The plants supply the bacteroids with sugars from the legume root cells and the bacteroids use these sugars to provide the energy for nitrogen fixation, providing a sophisticated symbiotic relationship. Interestingly, the critical bacterial enzymes are very sensitive to the presence of oxygen, being poisoned by even traces of free oxygen. However, it is the plant, not the bacteroid, which produces *leghemoglobin*, a compound that traps any oxygen present, thus protecting the bacterial enzymes from oxygen poisoning.

Competition is always a negative interaction for both parties and is most intense for resources such as space, food and water. As the population density increases, or the resource abundance decreases, competition increases and eventually the resource may become limiting for at least one of the participants. The negative features of competition may result in consequences such as reduced growth or fecundity, exclusion from a habitat or mortality; intraspecific competition can be particularly severe. However, ecosystems containing multiple species with overlapping niches can also produce intense competition. Competition is particularly strong for individual plants because most require the same mineral nutrients from the soil and require light for photosynthesis yet are unable to move when a resource becomes depleted. Agricultural practice today often involves the use of selective herbicides to reduce such competition from weed species.

Gause (1934) demonstrated that when two directly competing species within a simple, uniform, closed system (micro-organisms within a test tube) interact, one species will eventually completely exclude the other – which species wins depends upon the conditions within the system. This process is termed *competitive exclusion* and is typical of restricted environments. However, in patchy environments where each species can find local conditions that favour one species or the other, a species may persist even when its population densities are reduced by competition in other parts of its distribution.

## 5.2 Interactions with the environment

All organisms must be able to make internal adjustments in response to external changes in conditions, not only to survive but in order to grow and reproduce. All environments are in a state of almost constant flux, whilst each organism has a range of internal conditions that it must not exceed. Organisms normally survive environmental variations by one or more of the following responses.

- They can *resist* or *tolerate* the change, a process with significant limitations for both the degree and duration of the changes.
- They can establish new equilibria through the *regulation* of their internal environment (see homeostasis below) or by adapting their physiology to the conditions (*adaptation*).
- They can *move* (migrate) to a more suitable environment (*avoidance*).

All organisms exhibit response to stress, the general term given to the physiological condition where the level of an environmental condition or resource is outside the optimum range for that organism. The response of any species or individual to each environmental condition can be described as a generalised response curve (Figure 5.2.1) allowing the identification of optima and ranges for each combination of condition and species/individual. The shape of the curve will vary with species, life stage, season and physiological condition as well as with the nature of the stressor.

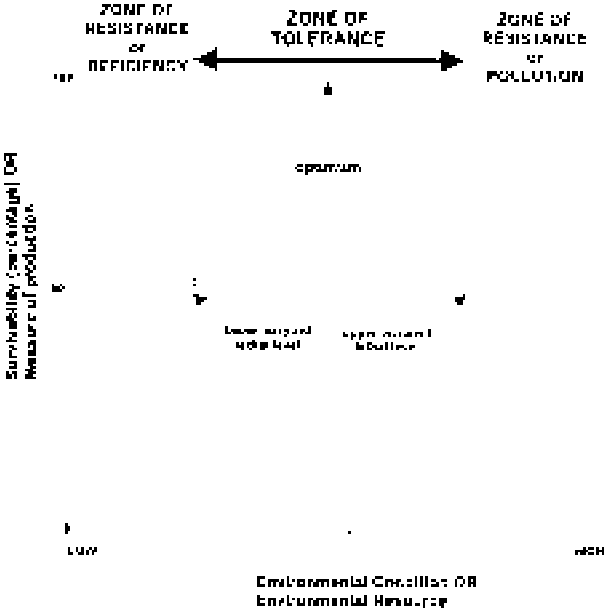

*Figure 5.2.1: Responses of organisms to stressors: A generalised response curve to show the main terminology associated with a response curve.*

*Tolerance* is largely a physiological response while *resistance*, although including physiological response, is significantly influenced by morphological and behavioural modifications. The evolution of body structures, for example exoskeletons, which provided a barrier between the environment and the extracellular fluid bathing the cells was important and allowed the evolution of mechanisms to control the composition of these fluids. This allowed the development of greater resistance and tolerance and, in particular, facilitated the transition from the sea to freshwaters and the land. Similarly, the ability to move provided mechanisms for reducing or avoiding negative conditions. Such modifications have evolved in response to potentially deleterious environmental conditions and are alternatives or supplements to the physiological homeostatic mechanisms.

Organisms are known from an enormous diversity of habitats from hot springs to the frozen polar regions, demonstrating the remarkable ability of organisms to evolve tolerance and compensation mechanisms to cope with such diverse conditions.

### *Box 5.2.1. Life in deserts: ways of surviving*

Deserts are very dry areas found in both temperate and tropical regions, characterised by low densities of life and low diversity. The low humidity of the desert atmosphere results in very wide daily temperature fluctuations, with cold nights and extremely hot days. This is a highly stressful environment and its unique condition of dry heat requires highly specialised morphological, physiological and behavioural adaptations. Organisms must both conserve water and control their temperature; these are conflicting demands since many organisms normally use evaporative cooling for temperature control. Plant cover is sparse but includes both perennial and annual species, all of which tend to have reduced leaves or no leaves, reducing transpiration and conserving water (*Xerophytes*). Succulent plants such as cacti, which store water, grow continuously and often secrete a thicker layer of cuticle over the surface to reduce water loss. A dense covering of epidermal hairs is also common and reduces the drying effects of air currents. Annual plants often adopt a strategy of carrying out their life cycle during the brief period when water may be present, evading the dry periods as desiccation-tolerant seeds. To reduce competition for water, some plants secrete substances from their roots or shed leaves that inhibit the establishment of other plants nearby (*allelopathy*). They frequently possess spines, thorns and toxins to minimise grazing by herbivores.

Desert animals tend to be small and most remain under cover or in burrows during the day, being active at night when it is cooler. Snakes and lizards are relatively common in deserts because their heavy skin prevents water loss and they produce mainly dry excretions. Most of their water derives from prey and from metabolic water – water produced during normal metabolism. Another famous example of an animal that can survive on metabolic water alone is the kangaroo rat. Larger animals such as camels and ostriches living in arid regions have heavy insulation (fur and feathers respectively) on their backs to keep out the heat from the sun. They are also physiologically very tolerant of dehydration: they can lose up to a quarter of their body water and yet make it up in a few minutes when water becomes available. Many desert animals also have unusually large tolerances of body temperature change, thus reducing the need for evaporative cooling and conservation of water.

### 5.3 Variation in life history

The life history of an organism comprises its patterns of growth, development and reproduction.

*Growth and development* are quite separate processes in most species. Rapid development leads to early reproduction and high rates of population increase; this is typical of pioneering species (weeds, etc.). However, many species living in transient or seasonal environments include periods of arrested development (*dormancy* and *diapause*) to provide a means of extending the life cycle through periods of adverse environmental conditions. Longevity is important in species with multiple breeding periods since it is related to the number of potential breeding periods.

*Reproduction* may take a variety of forms. Organisms may adopt diverse strategies in relation to the timing and effort of reproductive period. Thus, organisms such as trees and humans can have repeated reproductive activity over decades, while at the other extreme, organisms such as squid, freshwater eels and the salmon reproduce only once in a normal lifetime. Organisms also vary dramatically in their fecundity, a feature often associated with the method of fertilisation and the degree of parental care. Broadcast fertilisation requires a massive energetic investment in gametes, while copulation and parental care, for example in birds, allow that investment to be used for food reserves in relatively few eggs. Aftercare requires the use of resources for protection, suckling and foraging for food for developing young. Thus, the reproductive strategy of a species has dramatic consequences for both the energy budget of the individual and the abundance and population structure of that species.

*Dormancy* is a life history stage associated with resisting or tolerating periods of environmental adversity. Dormancy of some kind occurs in almost all types of organisms and it may be:

- *predictive*, that is it occurs in advance of the adverse conditions and is usually genetically programmed. This is typical of predictable seasonal environments where the temperature or photoperiod can be used as environmental cues.
- *consequential*, that is it occurs in response to prevailing conditions and is typical of organisms from unpredictable environments.

Generally, dormancy is a physiological state of minimal metabolic activity allowing an organism to avoid poor conditions or resource shortages, or both. Dormancy may be *facultative* – optional but related directly to prevailing conditions – or *obligate* – usually associated with a particular life stage, for example plant seeds. It exists as a variety of forms including:

- *resting spores* or buds found in a wide diversity of forms with over-wintering, or drought/temperature-resistant stages in bacteria, fungi, plants and lower animals
- *diapause*, a form of dormancy typically found at a specific stage in an insect life history and involving complete cessation of growth and development together with suspended metabolism
- *hibernation*, a period of inactivity in mammals associated with physiological changes resulting in a lowering of the metabolic rate to conserve energy during periods of environmental extremes
- *aestivation*, a period of inactivity associated with hot, dry periods during which the organism remains in a state of torpor with a reduced metabolic rate. This occurs in lungfish and amphibians such as desert frogs.

These factors have significant ecological consequences for ecological change such as that associated with colonisation, succession and stability. Populations of slow-growing species tend to be limited in number by the environment's carrying capacity (K) and are termed *K-strategists*. They usually live in the stable, predictable environments typical of climax communities. Populations of species characterised by very rapid growth and reproduction, often followed by sudden and large declines in population size, are called *r-strategists* since they have a high intrinsic rate of increase (r). They are typical of unpredictable and rapidly fluctuating environments and are often called opportunists, being also typical pioneering species in the early stages of ecological succession.

### 5.4 Homeostasis

*Homeostasis* (the process of maintaining internal constancy) maintains intracellular and extracellular fluids at relatively constant ionic and osmotic compositions even when the external conditions fluctuate considerably. Homeostasis is best demonstrated by mammals and birds, since in these organisms the evolution of internal systems for control and regulation of the key physiological processes is best developed. The evolution of homeostatic mechanisms was vital for the development of diverse form and function and to the colonisation of freshwater and terrestrial habitats. Homeostasis also allows biochemical systems to become more efficient by adapting to operate within relatively narrow ranges of physicochemical variables. When the external environment varies, there are two basic patterns of response. These are:

- *conformation*, where the internal variables fluctuate directly with the external environment and survival then depends on cellular resistance to damage;
- *regulation*, where internal variables are maintained at levels different from that of the environment, albeit at a significant energy cost.

In Figure 5.4.1, these two types of responses are shown graphically for the response to osmotic variation. The appropriate descriptive term is produced by adding a prefix to the variable name: hence for temperature, the relevant terms are thermoconformation and thermoregulation. Another important terminology relating to physiological constancy is the distinction between poikilothermic forms, those with variable internal temperatures (often called cold-blooded), and homeothermic forms which have relatively stable, usually raised internal temperatures (often called warm-blooded). The prefixes *poikilo* and *homeo* apply to other physiological variables too (as in, for example, poikilo-osmotic). Animals that obtain their body heat from the environment are properly termed *ectotherms* while those that have internal mechanisms for heat production are termed *endotherms*.

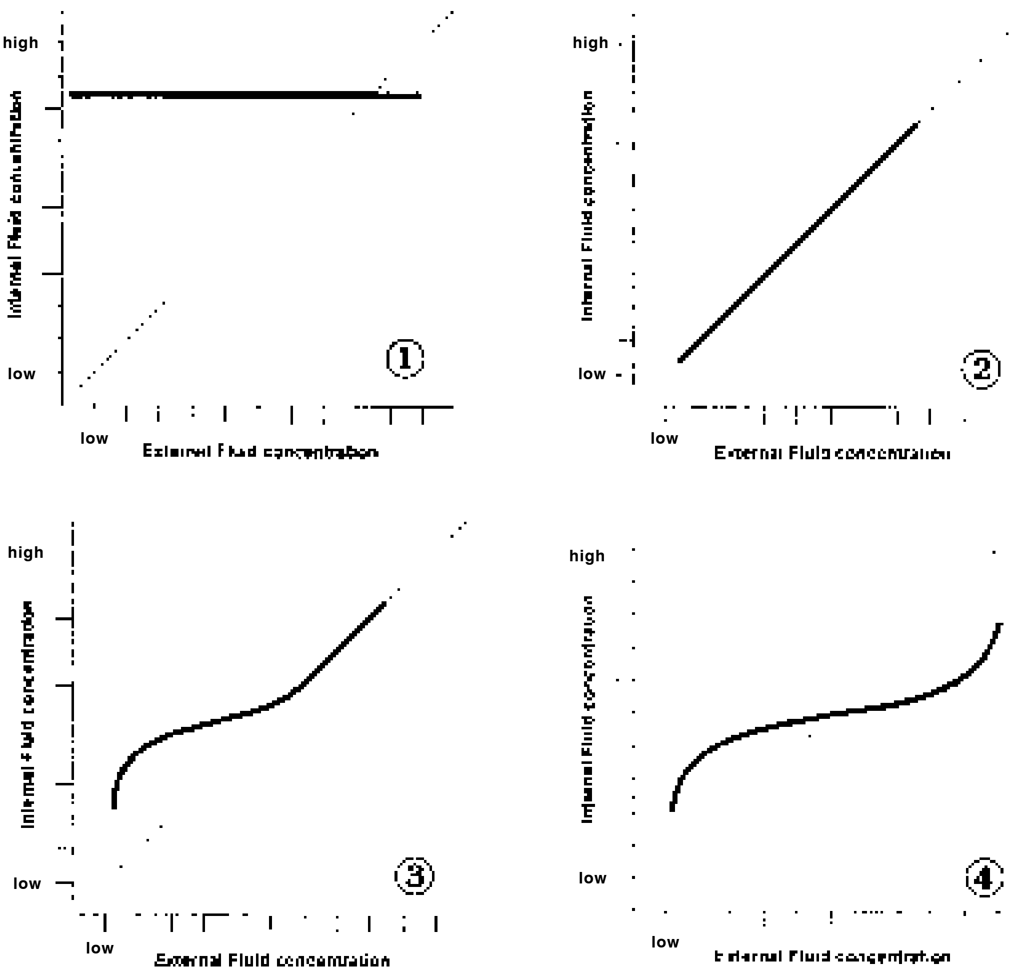

*Figure 5.4.1: Four generalised types of osmoregulatory response: 1. Perfect osmoregulation; 2. Perfect osmoconformer; 3. Hyperosmoregulation in dilute media; 4. Both hyper- and hypo-osmoregulation. The dotted line represents the line of iso-osmicity.*

The significance of these two alternative ways of responding to environmental changes is clear. Conformers tend to be restricted in their potential distribution unless they also possess mechanisms for avoidance of the problem: the ability of the osmo-conforming mussel to penetrate estuaries is founded on its ability to shut its shell valves to excluded water of unsuitable salinity. However, when in this protected state, it cannot carry out normal respiration or feeding activity so this can only be a very short-term strategy. Regulators, however, effectively carry life-support systems around to prevent environmental conditions being so limiting – this usually requires a lot of energy but frees the organism to roam relatively freely and thus potentially to exploit habitats from which conformers would be excluded.

The energy obtained by feeding has to be allocated to a diverse array of functions (see Section 1.2) from foraging (or obtaining nutrients) and avoiding predation, to growth and reproduction. Homeostatic mechanisms add significantly to this burden and such organisms usually require to consume relatively larger amounts of food to sustain the homeostatic mechanisms. Thus, large, cold-blooded reptiles such as crocodiles may be sustained for long periods on one prey item while the warm-blooded mammals and birds require large and frequent supplies of appropriate food. However, endothermy has many benefits that help in this requirement: endotherms are relatively unaffected by periods of cold such as occur at night, for example, and can forage for more sluggish ectotherms throughout the day if necessary. Thus, endothermy carries an energy burden but opens up many otherwise unavailable niches for foraging.

# 6. Changes to ecosystems

## 6.1 Changes in complexity

All ecosystems exhibit a diversity of complexity reflected by the number of species present, population sizes, biological productivity, variety of habitats and niches, and complexity of food webs. Communities are always changing and this change in composition and form, primarily of the vegetation, is usually from simple to complex in a process known as ecological succession. Succession is the non-seasonal, directional and continuous pattern of colonisation and extinction at a site by populations of species. It typically proceeds from immature, rapidly changing, unstable communities populated by pioneering, opportunistic r-strategists to more mature, self-sustaining and stable communities dominated by K-strategists. However, this idealised sequence is easily and frequently disrupted by major natural events or by anthropogenic (human) influences and the modern concept recognises that it is sometimes reversible.

A useful categorisation of types of succession follows:

- *Autogenic* succession is the natural sequence of changes resulting from biological processes that modify conditions and resources. It is divisible into:
  - *primary succession*, which occurs on barren habitats where organisms gradually colonise the area and, in so doing, modify it. Such habitats are created by major geophysical events and involve colonisation by pioneer species such as microbes, mosses and lichens. Such species gradually modify the environment so that new niches occur. (Figure 6.1.1).
  - *secondary* succession, which is more common and begins with the disturbance, natural or by man, of an existing community. This includes habitats subject to man's impact, such as burned and cut forests or abandoned farmland.
- *Allogenic* succession occurs as a result of changing external geophysical forces, such as climatic extremes and astronomical events.
- *Degradative* succession (heterotrophic succession) is related to the changes associated with decomposition processes.

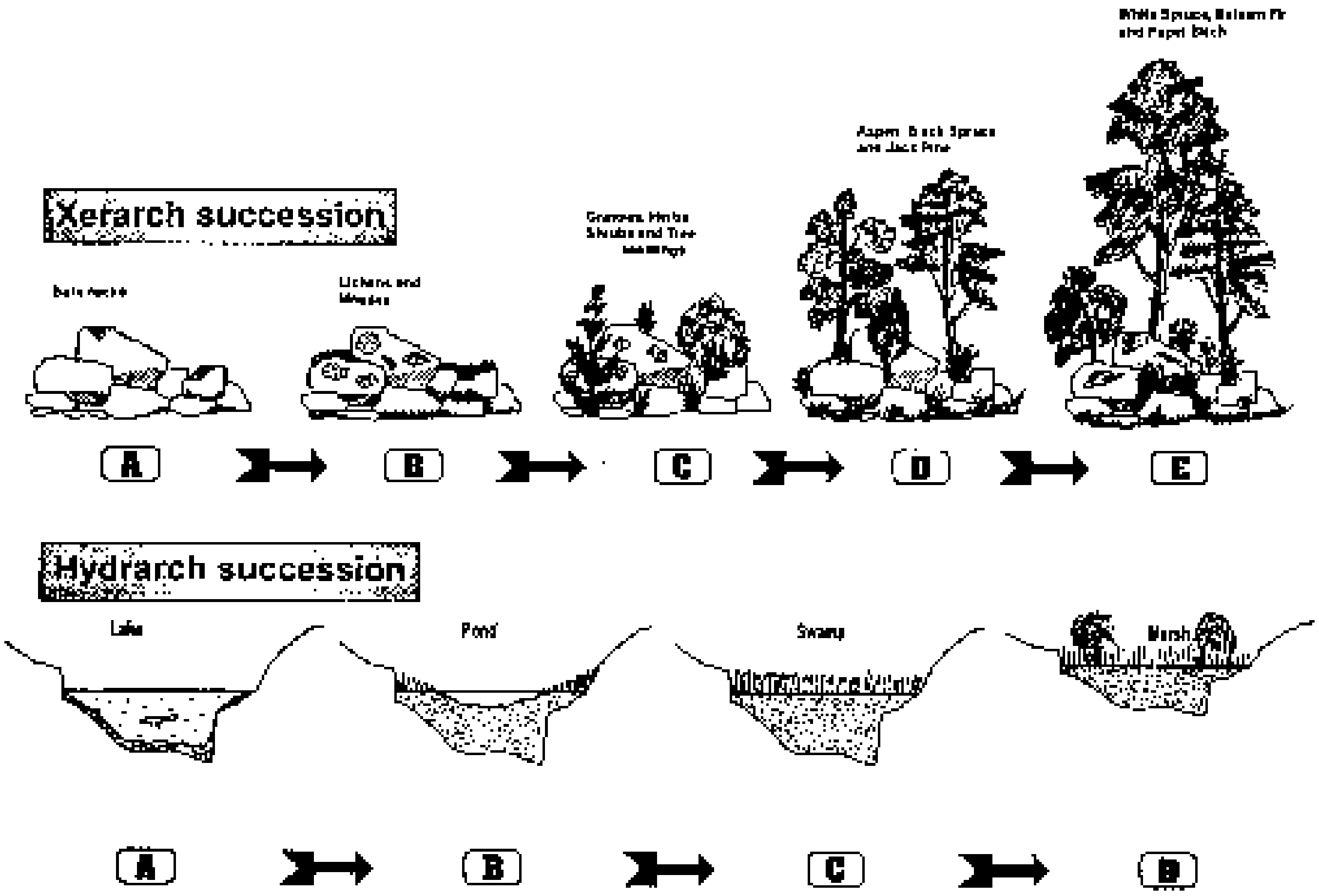

*Figure 6.1.1*: *Diagrammatic representation of the main stages in the two main types of succession: A. Xerarch succession; B. Hydrarch succession.*

Limited complexity is typical of naturally stressed communities and ecosystems that are subject to varying environmental conditions, for example estuaries. Loss of complexity in ecosystems is also typical of the stressed communities associated with polluted habitats that may result from eutrophication or toxic pollution. Habitats subject to oxygen depletion – natural (autumn) or pollution-induced – exhibit similar loss of diversity. Stressed habitats of all kinds typically show a reduction in species richness (Figure 6.1.2) but those species that are present are often present in large numbers due to the relative lack of interspecific competition in such habitats.

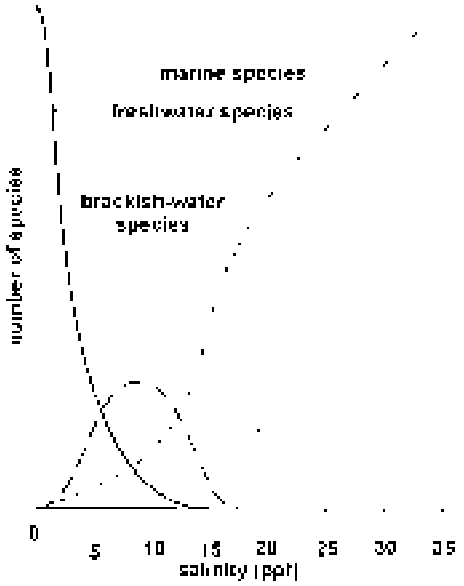

*Figure 6.1.2: The effects of salinity variation on the nature and abundance of species.*

A reduction in complexity also results from habitat destruction. Tropical rainforests are especially vulnerable to clear-cutting because most of their energy stores and nutrients are found above the ground. Recovery is rare and tends to lead to totally altered systems. Temperate forests, where the nutrient resources are mainly in the soil, can survive clearing activities much better, and secondary succession will often restore the system over time. Loss of diversity is also associated with modern agricultural practices typified by the development of monocultures of crops.

## 6.2 Effects of intensive food production

Monoculture is a form of agriculture or forestry in which a single species, often selected for its productivity and/or disease resistance, is cultivated over a large area for economic efficiency. Monoculture is often associated with the destruction of natural habitats. The economic justifications for such a strategy are fairly obvious but this process is fraught with risks. Most land is cultivated by replacing the naturally diverse communities with single crop or tree species. This often causes the leaking of nutrients from the land (resulting in the need to use chemical fertilisers) and, in regions such as the rainforests, the destruction of the soils. Much effort is also expended in protecting these crops from the inevitable invasions of pests. These include weeds (unwanted pioneer plant species that typically occupy the same niches as the crops), insect and other animal pests, and pathogenic (disease-producing) fungi, bacteria, or viruses. The dangers of monocultures are clear when predator–prey interactions are considered.

Experience shows that simplified ecosystems are very vulnerable to difficulties because they represent dense and abundant aggregations of the hosts of parasitic or disease-producing organisms. The advantages of diversity and physical separation in diverse communities are lost. The result is a potential for massive population explosions of pest species that frequently have short generation times and rapid reproduction rates. The usual solution to this problem is the protection of crops by the use of pesticides or, more rarely, some form of biological control by a natural predator.

The use of diverse chemicals to overcome the problems of intensive methods of agriculture and forestry also produces problems of its own. The substances used are frequently potentially toxic to a variety of other species, including man and, unless very judiciously used, represent a threat beyond the confines of their intended usage. Natural selection in rapidly breeding pests and disease-causing species has resulted in the development of genetic resistance to chemical pesticides. This leads to the use of stronger pesticide concentrations and the development of new toxic substances. Monoculture also encourages an increase in field size, which itself results in the depletion of hedgerows that provide shelter and habitats for a diverse flora and fauna.

## 6.3 Increase in energy needs

The biological world is driven almost entirely by solar radiation, captured by plants and thus incorporated into food webs; only relatively rare chemosynthetic communities, for example deep-sea vent communities, are not dependent upon the sun. The major sources of primary energy for human populations are the fossil fuels (coal, oil and gas), nuclear fuels and hydro-power. Each form of energy generation has its own environmental consequences. In addition, the fossil fuels are clearly finite in character and will require conservation in the long term.

Renewable energy sources, defined as those that can be harnessed without depletion, include solar, wind, wave, tidal, hydro, geothermal and biomass energy production. Note that with the exception of geothermal power, all the other sources derive their energy directly or indirectly from the sun. However, they are usually used to meet only relatively local energy requirements.

Perhaps the most important environmental consequences of the industrial age have been:

- the intensive production of potentially toxic wastes as a result of the extensive use of chemicals, many of which are new to nature (see Section 6.4)
- the release of ozone-depleting chemicals into the upper atmosphere leading to the development of the ozone hole and resulting in increasingly destructive levels of ultra-violet light at the surface.
- the extensive release of greenhouse gases. These are currently believed to be exacerbating the vital, natural greenhouse effect to produce global warming with its diverse environmental consequences including climate change.

The greenhouse effect is responsible for the maintenance of the planet's surface temperature at about 25 °C, estimated to be some 33 °C warmer than if the effect were not present! Although carbon dioxide is the focus of much of the attention in relation to the control of global warming (this is best termed the ***enhanced greenhouse effect***), the main natural greenhouse gases include water, methane and nitrous oxide as well as carbon dioxide. To these must be added the man-made chlorofluorocarbons (CFCs), such as those commonly used in refrigeration, which are also responsible for the unrelated ozone depletion. Estimates of their relative importance suggests that carbon dioxide accounts for an estimated 60% of the enhanced greenhouse effect, methane 15%, nitrous oxide 5%, tropospheric ozone 8% and CFCs 12% (Rodhe, 1990). However, the relationships are complex and the significance of man's inputs for global warming is disputed. The biological effects of resulting climate change could be profound since climate is one of the principal conditions defining the niche requirements of most species. Changes in both abundance and distribution of species will result. A good example already described is the widespread phenomenon of 'coral bleaching' (see Section 5.1), which is the result of the warming of seawater. This drives out the symbiotic zooxanthellae from corals resulting in their death.

## 6.4 Pollution

One of the important consequences of trophic interactions is the transfer and recycling of materials between trophic levels. The transfer of materials through the food web is of considerable significance since it is by this means that many mineral, vitamins, etc. are obtained and conserved. However, many undesirable materials may also be incorporated into this process and this can result in the accumulation of materials to concentrations where a deleterious biological effect may occur.

Any chemical is potentially toxic if present in sufficient concentration. Elements most frequently associated with toxicity from environmental exposures include the heavy metals cadmium (Cd), mercury (Hg), chromium (Cr), silver (Ag), copper (Cu), cobalt (Co), iron (Fe), nickel (Ni), lead (Pb) and tin (Sn), and lighter elements such as aluminium (Al), arsenic (As) and selenium (Se). To these elements must be added the immense number of compounds, both natural and synthetic (organic chemicals mainly), known to exert toxic effects, for example DDT, malathion and tributyl tin.

Two trophically related processes exacerbate the problem of toxic materials in the environment, namely *bioconcentration* and *biomagnification* (Figure 6.4.1). Materials from the environment accumulate (concentrate) within an individual through a variety of biological processes usually associated with feeding or respiration. Thus the gills of a mussel act as an absorptive organ for heavy metals while they are being used for feeding and respiration. Such materials may then move to storage sites within the body where they may further accumulate and thus concentrate. Bioconcentration factors of several orders of magnitude occur for some substances such as mercury.

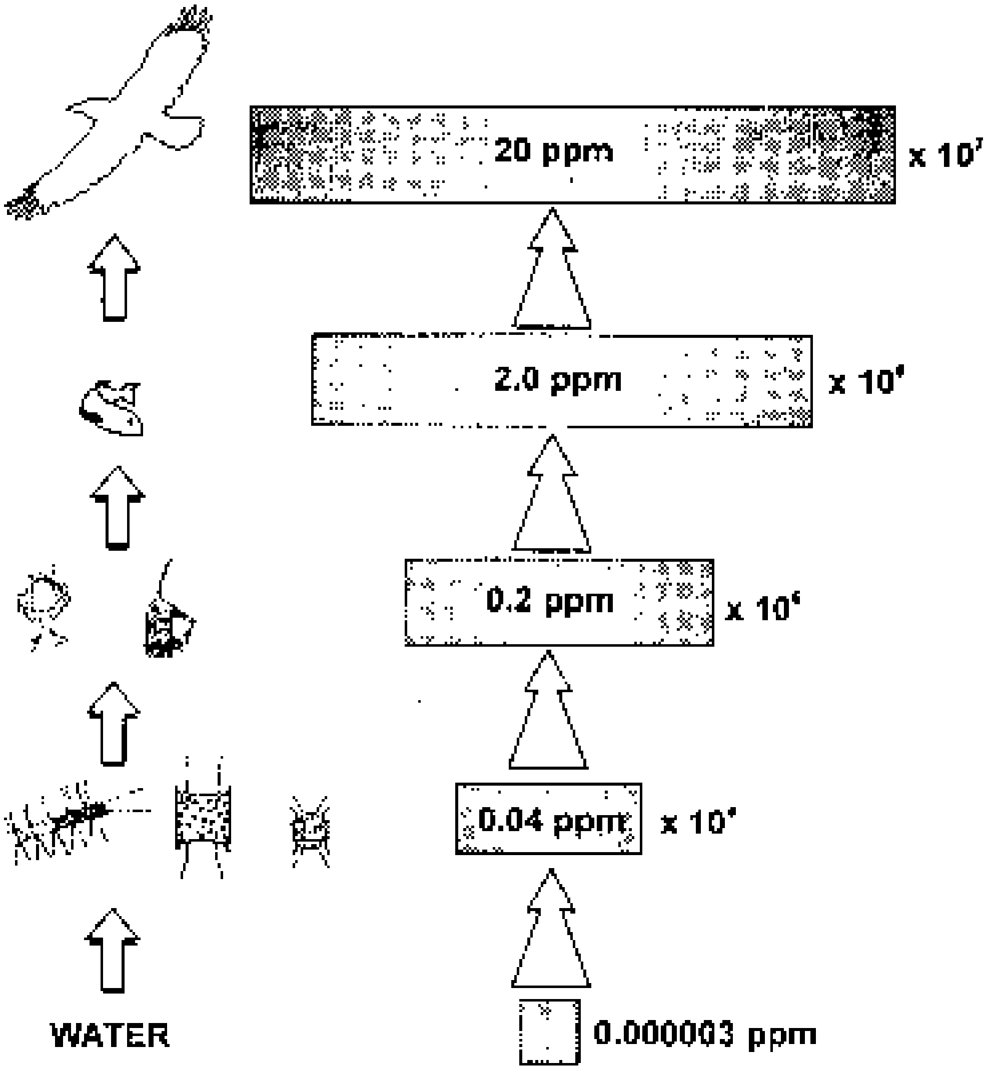

***Figure 6.4.1****: Biomagnification of DDT along an aquatic food chain. The concentration factors (relative to that in the water) are shown alongside the boxes. The levels in the top predator may be seven million times greater!*

The second means of concentrating materials is through the eating of organisms, thus incorporating their body burden of the material into the body of the consumer. This process may occur at each trophic level so that, in the top predator, substances that seem innocuous at their original environmental concentrations may concentrate to levels at which toxic effects are significant (biomagnification). The story of DDT is a very good example (Box 6.4.1).

### *Box 6.4.1. The DDT story and its warnings*

DDT (**D**ichloro**d**iphenyl**t**richloroethane) is the best known of a number of chlorine-containing pesticides. It was used extensively in the 1940s and 50s to kill malarial mosquitoes and the lice that spread typhus. As such, it saved millions of lives. Unfortunately, experience proved that DDT had a number of unfortunate and unpredicted ecological consequences, so much so that its use was banned in the USA in 1972 and by 1980 its export from the USA ceased. However, its manufacture and use in less developed countries continues. The main lessons learnt from experience with DDT are listed here.

- DDT is *persistent*, being broken down only very slowly by decomposers. It has a *half-life*, the time taken for half of a substance to degrade, of about three years; this results in environmental accumulation and distribution of the substance. DDT is now found everywhere in the world from the Antarctic ice to the bodies of humans.

- DDT was the first pesticide to which diverse insect pests developed a *resistance* by evolutionary selection for resistant genotypes in exposed populations. Thirty-four species of the malaria-carrying *Anopheles* mosquito are known to be DDT resistant.

- The primary breakdown product of DDT is DDE (**D**ichlorodiphenyl**di**chloro**e**thane), produced by dechlorination reactions that occur in alkaline environments or enzymatically in organisms. Unfortunately, DDE is almost as persistent as DDT and is responsible for shell-thinning in predatory birds. Breakdown products must always be considered when evaluating the risks associated with chemical releases.

- Bioaccumulation, the retention or building-up of non-biodegradable or slowly biodegradable chemicals in the body to produce what is termed a body-burden of a substance, is an important process, especially for persistent materials. DDT is particularly soluble in lipids but not very soluble in water (less than 0.1 ppm), and both it and its metabolite DDE readily accumulate in the fatty body reserves of organisms.

The problem of bioaccumulation is compounded in aquatically based food chains by *biomagnification* (biological amplification), whereby the concentration of a chemical increases at each trophic transfer. This process can result in concentration factors between trophic levels of one or two orders of magnitude, and for heavy metals such as mercury, factors of a thousand times have been reported. Concentration factors along the entire food chain may result in the top predator containing several million times the concentrations in the water column.

Although it was clear that high concentrations of DDT would be lethal, other *sub-lethal* mechanisms of ecological and public health impact have become evident. This includes a reduction in resistance to diseases, parasites and predators, and a reduction in reproductive capability. Populations of top predator birds such as fish-eating ospreys and bald eagles and rabbit-eating birds of prey declined dramatically in the 1960s. This was not only a consequence of deaths resulting from lethal concentrations of DDT/DDE being accumulated but also because of loss of eggs due to egg-shell thinning and shells breaking. This was because DDE reduces the amount of calcium in the shell.

Another important biological process is the *biotransformation* of materials, often during the degradative metabolic processes of organisms, particularly micro-organisms. This is useful when it is part of the natural degradation and decomposition processes that are fundamental for materials recycling, a process vital to the sustainability of life. However, some transformations are deleterious. The transformation of relatively low toxicity inorganic mercurial ions to the highly toxic methyl mercury ions (Figure 6.4.2) by microbial activities in the marine sediments of Minimata Bay in Japan is a good example, but many more can be found in the literature.

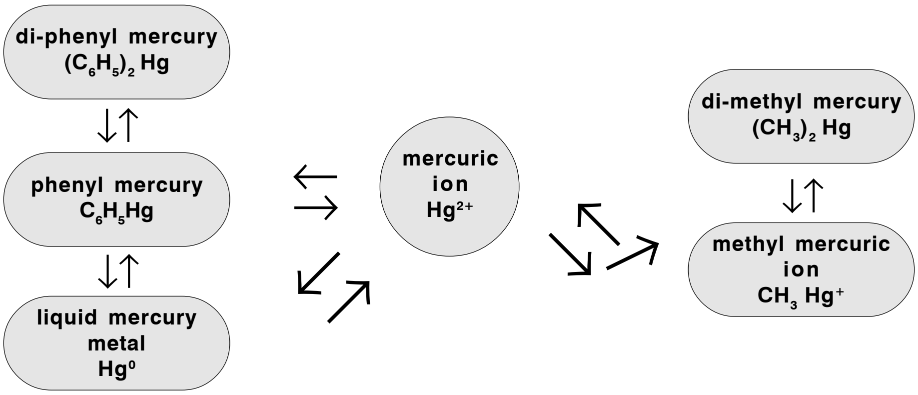

***Figure 6.4.2**: The biotransformations of mercury from metallic mercury ($Hg^0$) to the very toxic methyl mercuric form.*

Another important form of pollution is that associated with the removal or lowering of oxygen concentrations as a result of organic degradation or direct chemical oxidations. The input of large quantities of organic matter, either as intensive farming wastes and silage, as sewage or as natural leaf debris in autumn, can have devastating effects on the flora and fauna of aquatic systems as a result of degradative oxygen depletion.

Not all species respond in the same way to a pollutant and it is important to recognise that for any particular pollutant there will be very sensitive and less sensitive species. Thus organic tin (TBT) has devastating effects on oysters and some other molluscs such as dog whelks (*Nucella lapillus*) whilst having negligible effects on most other species! Differential sensitivity is a very important concept in pollution studies and would be an appropriate activity for simple experimentation.

Alien (also introduced or exotic) species represent another form of pollution and have become common aspects of local landscapes. Such species may be introduced intentionally or accidentally and they tend to be good dispersers and, therefore, colonisers. The most successful ones are also competitively superior to indigenous species, often lacking natural predators in their new location. Others may find an ‘open’ niche to exploit. The worst introductions have included goats, pigs, cats and rats to islands around the world and these have often resulted in the widespread destruction of habitats and the loss of endemic species.

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