that the chicks often died in the egg. Conservationists charged with restoring the bald eagle population had to find a way to increase the birds' birth rate. The banning of DDT achieved this end.

5.1.1 What is an individual?

unitary and modular organisms

A population is characterized by the number of individuals it contains, but for some kinds of organism it is not always clear what we mean by an individual. Often there is no problem, especially for *unitary* organisms. Birds, insects, reptiles and mammals are all unitary organisms. The whole form of such organisms, and their program of development from the moment when a sperm fuses with an egg, is predictable and *determinate*. An individual spider has eight legs. A spider that lived a long life would not grow more legs.

But none of this is so simple for *modular* organisms such as trees, shrubs and herbs, corals, sponges and very many other marine invertebrates. These grow by the repeated production of modules (leaves, coral polyps, etc.) and almost always form a branching structure. Such organisms have an architecture: most are rooted or fixed, not motile (Figure 5.1). Both their structure and their precise program of development are not predictable but *indeterminate*. We could count the individual trees in a forest, but would this signify the 'size' of the tree population? Not unless we also noted whether the trees were young saplings (few leaves and branches each), or old individuals, each with many more such modules. Indeed, it may make more sense not to count the individual trees themselves but the total number of modules instead.

modular organisms are themselves populations of modules

In modular organisms, then, we need to distinguish between the genet – the genetic individual – and the module. The *genet* is the individual that starts life as a single-celled zygote and is considered dead only when all its component modules have died. A *module* starts life as a multicellular outgrowth from another module and proceeds through a life cycle to maturity and death even though the form and development of the whole genet are indeterminate. We usually think of unitary organisms when we write or talk about populations, perhaps because we ourselves are unitary, and there are certainly many more species of unitary than of modular organisms. But modular organisms are not rare exceptions and oddities. Most of the living matter (biomass) on Earth and a large part of that in the sea is of modular organisms: the forests, grasslands, coral reefs and peat-forming mosses.

5.1.2 Counting individuals, births and deaths

Even with unitary organisms, we face enormous technical problems when we try to count what is happening to populations in nature. A great many ecological questions remain unanswered because of these problems. For example, resources can only be focused on controlling a pest effectively if it is known when its birth rate is highest. But this can only be known by monitoring accurately either births themselves or rising total numbers – neither of which is ever easy.

the difficulties of counting

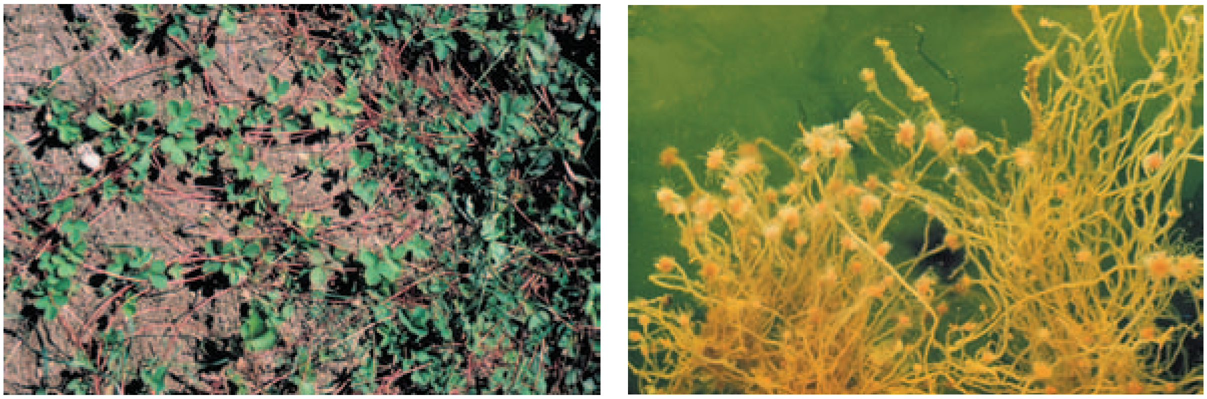
If we want to know how many fish there are in a pond we might obtain an accurate count by putting in poison and counting the dead bodies. But apart from the questionable morality of doing this, we usually want to continue studying a population after we have counted it. Occasionally it may be possible to trap alive

Figure 5.1

Modular plants (on the left) and animals (on the right), showing the underlying parallels in the various ways they may be constructed. (a) Modular organisms that fall to pieces as they grow: duckweed (*Lemna* sp.) (© John D. Cunningham) and *Hydra* sp. (© Larry Stepanowicz). (b) Freely branching organisms in which the modules are displayed as individuals on 'stalks': a vegetative shoot of a higher plant (*Lonicera japonica*) with leaves (feeding modules) and a flowering shoot (© Visuals Unlimited), and a hydroid colony (*Obelia*) bearing both feeding and reproductive modules (© Larry Stepanowicz).

all the individuals in a population, count them and then release them. With birds, for example, it may be possible to mark nestlings with leg rings and ultimately recognize every individual (except immigrants) in the population of a small woodland. It is not too difficult to count the numbers of large mammals such as deer on an isolated island. But it is very much more difficult to count the numbers of lemmings in a patch of tundra because they spend a large part of the year (and

(c)



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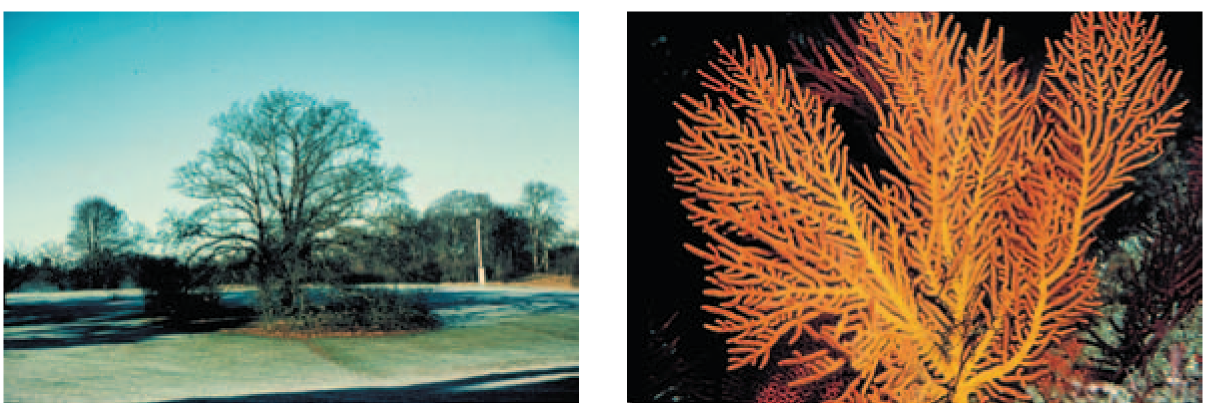


Figure 5.1 (*cont.*)

(c) Stoloniferous organisms in which colonies spread laterally and remain joined by 'stolons' or rhizomes: a single plant of strawberry (*Fragaria*) spreading by means of stolons (© Science VU) and a colony of the hydroid *Tubularia crocea* (© John D. Cunningham). (d) Tightly packed colonies of modules: a tussock of the spotted saxifrage (*Saxifraga bronchialis*) (© Gerald and Buff Corsi) and a segment of the hard coral *Turbinaria reniformis* (© Dave B. Fleetham). (e) Modules accumulated on a long, persistent, largely dead support: an oak tree (*Quercus robur*) in which the support is mainly the dead woody tissues derived from previous modules (© Silwood Park) and a gorgonian coral in which the support is mainly heavily calcified tissues from earlier modules (© Daniel W. Gotshall).

may reproduce) under thick snow cover. And most other species are so small, or cryptic, or hidden, or fast moving that they are even more difficult to count.

estimates from representative samples

Ecologists, therefore, are almost always forced to estimate rather than count. They may estimate the numbers of aphids on a crop, for example, by counting the number on a representative sample of leaves, then estimating the number of leaves per square meter of ground, and from this estimating the number of aphids per square meter. Sometimes more complex methods are used (Box 5.1), and at other times we may rely on indirect 'indices' of abundance. These can provide

5.1 Quantitative aspects

5.1 QUANTITATIVE ASPECTS

Mark–recapture methods for estimating population size

An estimate of the size of a population can sometimes be made by capturing a sample of individuals, marking them in some way (paint spots, leg rings) and then releasing them. Later, another sample is captured, and the proportion that is marked gives some estimate of the size of the whole population (Figure 5.2). For example, we might capture and mark 100 individuals from a population of sparrows and release them back into the population. If we later sample a further 100 individuals from the population and find half are marked, we could argue in the following way: half the sample are marked; the sample is representative of the whole population; therefore half the population are marked; 100 individuals were given a mark; therefore the whole population is composed of about 200 individuals. But this technique of mark and recapture is far less straightforward than it appears at first sight. There are many pitfalls in the sampling process and in interpretation of the data. Suppose, for example, that many of the individuals we marked died between our first and second visits. Modifications of the method would be needed to take account of this. For many organisms, however, it is the only technique that we have to estimate the size of a population.

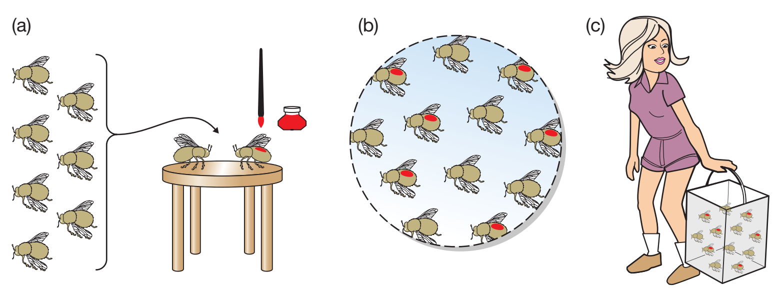
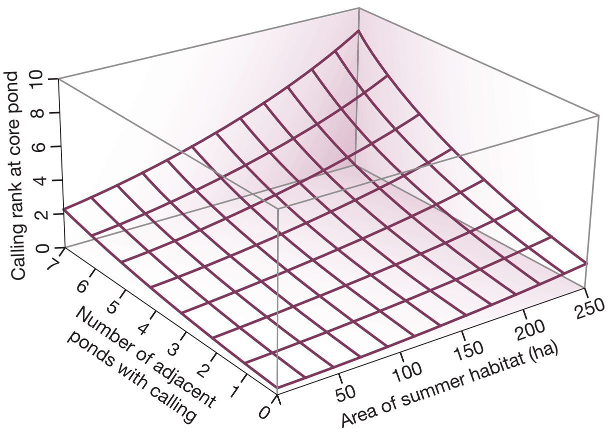


Figure 5.2

The mark and recapture technique for estimating the size of a population of mobile organisms (in simplified form). (a) On a first visit to a population of unknown total size N, a representative sample is caught (r individuals) and given a harmless mark. (b) These are released back into the population, where they remix with the unknown number of unmarked individuals. (c) On a second visit, a further representative sample is caught. Because it is representative, the proportion of marks in the sample (m out of a total sample of n) should, on average, be the same as that in the whole population (r out of a total of N). Hence N can be estimated.



AFTER POPE ET AL., 2000

Figure 5.3

The abundance (calling rank) of leopard frogs (*Rana pipiens*) in ponds increases significantly with both the number of adjacent ponds that are occupied and the area of summer habitat within 1 km of the pond. Calling rank is the sum of an index measured on four occasions, namely: 0, no individuals calling; 1, individuals can be counted, calls not overlapping; 2, calls of <15 individuals can be distinguished with some overlapping; 3, calls of ≥ 15 individuals.

information on the relative size of a population, but usually give little indication of absolute size. As an example, Figure 5.3 shows how the abundance of Canadian leopard frogs was affected by the number of occupied ponds and the amount of summer (terrestrial) habitat in their vicinity. Here, frog abundance was estimated from the 'calling rank': whether there were no frogs, 'few', 'many' or 'very many' frogs calling on each of four occasions. Despite their shortcomings, even indices of abundance can provide valuable information.

Moreover, as we have already noted, for modular organisms it is often not even clear what it is we should be counting.

5.2 Life cycles

5.2.1 Life cycles and reproduction

If we wish to understand the forces determining the abundance of a population of organisms, we need to know the important phases of those organisms' lives: that is, the phases when these forces act most significantly. For this, we need to understand the sequences of events that occur in those organisms' life cycles.

There is a point in the life of any individual when, if it survives that long, it will start to reproduce and leave progeny. A highly simplified, generalized life history (Figure 5.4) comprises birth, followed by a pre-reproductive period, a period of reproduction, a post-reproductive period and then death as a result of senescence (though of course other forms of mortality may intervene at any time). The life histories of all unitary organisms can be seen as variations around this simple pattern, though a post-reproductive period (as seen in humans) is probably rather unusual.

the conflict between growth and reproduction

Some organisms fit several or many generations within a single year, some have just one generation each year (annuals) and others (perennials) have a life cycle extended over several or many years. For all organisms, though, a period of growth occurs before there is any reproduction, and growth usually slows down (and in some cases stops altogether) when reproduction starts. Growth and reproduction both require resources and there is clearly some conflict between them. Thus, as the perennial plant *Sparaxis grandiflora* enters its reproductive