Recruitment

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Introduction and Definitions

In its most general sense, 'recruitment' refers to the process of adding new individuals to a population or to a specific segment of that population (e.g., breeding or harvestable individuals) through reproduction, immigration, and stocking. Recruitment can be measured in numbers, biomass, or rate. In the context of population dynamics, recruitment includes both processes that add individuals to a given population: the birth and the immigration. Recruitment is consequently opposed by the two processes that measure loss of individuals from a population: the mortality and the emigration. The difference between additions and losses determines 'net recruitment'.

For a birth pulse population censused just before births, we can thus simply write the transition from a population of size N_t in year t to one of size N_{t+1} in year $t+1$ as

$$N_t + \text{birth}_t + \text{immigration}_{[t,t+1]} - \text{death}_{[t,t+1]}$$
$$- \text{emigration}_{[t,t+1]} = N_{t+1} \qquad [1]$$

which is equivalent to

$$N_t + \text{recruitment}_{[t+1]} - \text{death}_{[t,t+1]}$$
$$- \text{emigration}_{[t,t+1]} = N_{t+1} \qquad [1']$$

which is equivalent to

$$N_t + \text{net recruitment}_{[t+1]} = N_{t+1} \qquad [1'']$$

Equation [1''] can be arranged to demonstrate that the net recruitment rate in a given year (net recruitment$_{[t+1]}/N_{t+1}$) is equal to the 'per capita change' ($\lambda - 1$) where λ (or N_{t+1}/N_t) is the 'natural rate of increase' of the population. Finally, note that the natural log of λ corresponds to r, the 'exponential growth rate' of the population or 'Malthusian growth rate'. In most studies of population dynamics, the 'per capita change' ($\lambda - 1$), the natural rate of increase (λ), and the 'exponential growth rate' (r) are all used to measure the 'population growth rate'. Recruitment is thus central to population dynamics.

Most studies of population dynamics, however, use a more restricted definition of recruitment, the number of births that occur within a pulse minus the number of deaths and emigrations of those individuals before the next birth pulse. The estimate of recruitment thus crucially depends on the life cycle stage at which death and emigration are measured, so that some standardization is required when performing comparative analyses across populations or species. As the number of births within a given pulse corresponds to a 'cohort', the recruitment rate of a closed population (i.e., without immigration or emigration) corresponds to the proportion of individuals from a given cohort that are added to the population at some specific stage.

Measuring Recruitment

The measure of recruitment is critically dependent on the life history stage at which death and/or emigration of individuals is assessed. To illustrate this important point, we will consider for example a population of a large mammal in a temperate ecosystem. The births are highly synchronized over a short yearly pulse, producing one new cohort each spring. The 'life cycle graph' (**Figure 1**) describes the different stages that individuals may experience from birth to death. In our example, individuals may survive from birth to weaning (summer survival of juveniles), from weaning to 1 year of age (winter survival of juveniles), from 1 to 2 years of age (yearling survival), then each year from 2 to 7 years of age (prime-aged adult survival), and finally each year from 8 to the maximum longevity (senescent adult survival). Each cohort is the sum of newborns produced by 2-year-olds (primiparous females), and prime-aged and
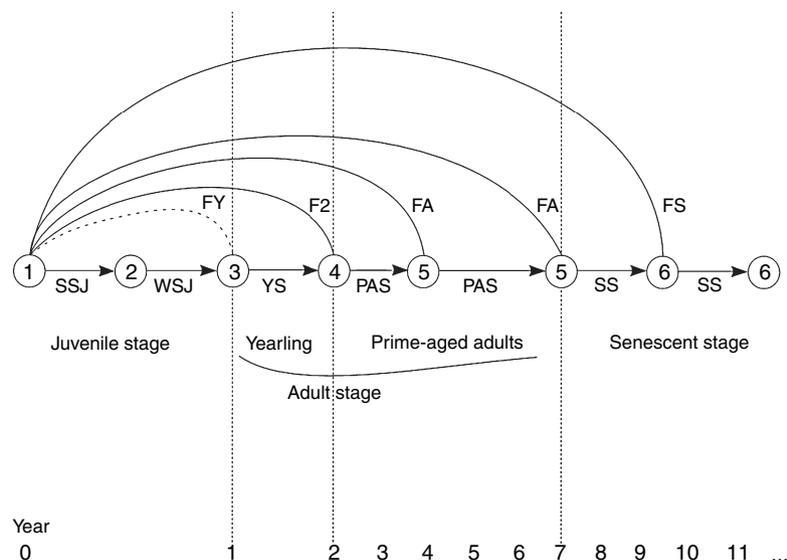
Figure 1 Life-cycle graph of a population of a temperate large mammal: (1) newborns, (2) weaned young, (3) yearlings, (4) 2-year-olds, (5) prime-aged adults, (6) senescent adults (older than 7 years). Straight lines indicate transitions (survival) from one age group to the next; curved lines indicate reproduction. These demographic rates describe the development of individuals through the life cycle. SSJ, summer survival of juveniles; WSJ, winter survival of juveniles; YS, yearling survival; PAS, prime-aged adult survival; SS, senescent survival; FY, fecundity of yearlings; F2, fecundity of 2-year-old females; FA, fecundity of prime-aged females; FS, fecundity of senescent females.

senescent females (mostly multiparous females). Recruitment can then be measured as the total number of newborns, the number of weaned juveniles (newborns that survive their first summer), the number of yearlings (newborns surviving to 1 year of age), or the number of 2-year-olds (newborns surviving to the age of primiparity). The choice of a given measure of recruitment will depend on the context of the study. For instance, in species with parental care, separating out costs of reproduction might be a relevant issue. Two traits determine the number of newborns produced by a given age class: the proportion of reproducing females and litter size. Let us consider a idealized population with neither emigration nor immigration. This population includes 100 adult females (i.e., potential breeders) of which 15 of 20 2-year-olds and all 80 older females give birth to an average of 1.8 newborns. Independent of maternal age, summer juvenile survival is 0.65, winter juvenile survival is 0.85, and yearling survival is 0.92. Those reproductive and survival rates would lead to the recruitment of 171 newborns, 111 weaned juveniles, 94 1-year-olds, and 87 2-year-olds. Consequently, our estimate of recruitment varies twofold depending on the stage at which it is assessed. It is therefore important to describe recruitment units (e.g., newborns surviving to a given number of months of age). In this example, the stage at which proportionally most mortality occurs is summer juvenile survival so that the weaning period is the dominant filter in the life cycle. As a rule of thumb, to assess the importance of recruitment for population dynamics, it should be measured at the end of the life cycle stage with the greatest mortality.

Variation in Recruitment: Causes and Magnitude

The definition of recruitment is critically important to assess not only which factors affect it but also the magnitude of its variability over space and time. In plants and marine organisms, dispersal plays a prominent role in recruitment. Even in marine ecosystems often considered as open systems in which recruitment is from outside the local population, a larger than expected proportion of juveniles may return to their natal population ('self-recruitment'). Obviously, sampling problems currently impede progress in the assessment of the impact of dispersing juveniles on population dynamics of marine organisms.

In most studies, independent of the taxon considered, recruitment has been reported to vary substantially in time and space in response to a large array of environmental and maternal factors. Thus, at birth, propagule (either larvae, eggs, seeds, or newborns) size strongly influences recruitment measured later on (e.g., at the end of the juvenile stage) in most studies, and, as a general rule at the intraspecific level, producing heavier/larger propagules is better. Similarly, between-cohort variation in the timing of births often accounts for variation in recruitment measured later on. While the relative advantage of being born early or late can be context specific, some general patterns can be identified. For instance, for most vertebrates of temperate ecosystems, those born early in the season are often more likely to recruit into the next life history stage than those born late.

Environmental conditions often drive variation in recruitment. In most case studies, the amount of predation, climatic conditions (e.g., drought for plants or terrestrial animals, temperature in marine organisms, reduced light for trees), physical and chemical properties of the ecosystem (e.g., exposition to chemical inducers that reduce growth and survival of juveniles), the prevalence of various diseases, population density, habitat quality, the availability of refuges, and the intensity of interspecific competition all markedly influence recruitment. Most of the time, several environmental factors interplay to shape recruitment, and their interaction can either increase or dampen recruitment variation. For instance, in flatfish, variation in habitat quality has been reported to lower rather than to increase recruitment variability. Besides these ecological sources of variation, recruitment can also vary as a direct consequence of the life history strategy. For instance, the high fecundity of weakly developed propagules leads to a random variation in mortality rates during early life history stages, and provides thereby the raw material for large fluctuations of recruitment in space and time, as illustrated by many exploited marine species. All empirical studies on annual plants, trees, marine invertebrates, and terrestrial or marine vertebrates have underlined that recruitment is a complex process involving the interaction of biotic and abiotic factors which operate at different temporal and spatial scales.

Assessing the Role of Variation in Recruitment on Population Dynamics

The influence of variation in recruitment relative to variation in mortality or emigration in determining variation in population size and growth has been analyzed in several taxa living across a range of ecosystems. There is no consensus on the relative importance of recruitment. In most terrestrial vertebrates, adult survival typically varies much less than recruitment through time, space, or with population density. In marine ecosystems, the 'recruitment limitation hypothesis' states that recruitment patterns account for most of the temporal or spatial variation in population abundance of most species. However, some studies of tropical reef fishes and of marine invertebrates have reported that changes in postrecruitment mortality rate and postsettlement processes can be more influential than changes in recruitment rate. Several methodological issues might account for such inconsistencies. Before we can safely identify the ecological and evolutionary causes of variation in the relative importance of recruitment on population dynamics, such problems have to be solved.

First, recruitment is not defined consistently among studies. Obviously different measures of recruitment will provide different answers. Early recruitment stages (i.e., number of propagules produced, early survival) are generally much more variable than late recruitment stages (i.e., late survival and settlement). The relative contribution of the different stages to recruitment variation, however, is rarely known and can vary from site to site for a given species. Moreover, the parameters describing the outcome of the different recruitment stages have a multiplicative, rather than an additive, influence on the whole recruitment process. Thus, under some conditions, the overall variation in recruitment will be much larger than the observed variation in any recruitment stage, whereas under other conditions, some compensation between recruitment stages could dampen the observed variability of recruitment. The contribution of the interactions among recruitment stages to changes in population abundance could be much higher than the contribution of the main effects of these stages. Serial autocorrelation among recruitment stages, although rarely assessed, is thus expected to play a major role in population dynamics.

Second, the analysis of the relative importance of recruitment on population dynamics strongly depends on the scale of analysis. Analyses at different scales answer different questions. The relative contribution of recruitment can be calculated from demographic analysis by performing a sensitivity or elasticity analysis. The question asked is then "By how much 'would' population growth 'change if' recruitment was increased or decreased by a given amount (sensitivity analysis) or a given proportion (elasticity analysis)?" Asking the same question for other processes (e.g., postrecruitment survival) will provide a measure of the relative contribution of recruitment to population dynamics. Note that this approach ignores the variation in recruitment observed in the field, because it only estimates a potential influence. In most cases the expected relative contribution of recruitment assessed from elasticity analyses reflects the position of the study species on the slow–fast continuum of life histories. Recruitment tends to exert a stronger influence on population dynamics in species in which individuals produce a large number of propagules early in their life and have short life span compared to species where individuals produce few propagules late in their life and have long life span. For example, the relative importance of seedling recruitment varies substantially between annual plants, perennial herbs, and shrubs and trees, being much larger in herbs than in woody plants.

The relative contribution of recruitment can also be used to answer a different question: "By how much does the 'observed' variation in population growth 'change in response to observed' changes in recruitment?" Asking the same question for other processes (e.g., postrecruitment survival) will also provide a measure of the relative contribution of recruitment to population dynamics. That approach accounts for the variation in recruitment observed in the field, so that the influence of both the observed variation (the larger the variation in recruitment, the higher its relative contribution, holding other demographic

processes constant) and the potential impact (the larger the elasticity or sensitivity, the higher the relative contribution of recruitment) of demographic processes are included. Using these approaches the relative contribution of recruitment is context specific and thereby less easy to predict from a species' life history than the expected contribution. It is quite straightforward to understand why predicting the potential impact of changes of a demographic rate on the population growth rate is easier than predicting the relative contribution of the same demographic rate to observed changes in population growth. In the first case, we perturb all demographic rates by the same proportional amount, while in the second the observed perturbations vary between demographic rates. However, some general patterns could exist in relation to the taxa studied or to the demographic status of the populations studied. For instance, most populations of passerine birds in the UK have been reported to be limited mainly through recruitment to the breeding population. In both marine invertebrates and large herbivores, the relative importance of recruitment versus adult survival could decrease with increasing densities. More studies are required to assess the general relevance of such findings. Depending on changes in environmental conditions, there can be much variation in the relative contribution of recruitment among, but also within, populations of a given species. Moreover, depending on whether we assume a perturbation (potential impact) or measure observed perturbations (relative contribution) of demographic rates, the importance of recruitment relative to other demographic processes can strongly differ for a given study.

Immediate and Delayed Effects of Recruitment Variation on Population Dynamics

As discussed above, temporal variation in recruitment has major influences on population dynamics. So far, however, we only considered the 'numerical effects' of recruitment fluctuations. Thus, depending on the suitability of the environmental conditions when a cohort is produced, a variable number of propagules will survive throughout the different recruitment stages. That simple process can generate complex dynamics, especially in populations that are strongly age- or stage-structured. The signature of one major change in the number of recruits from a cohort can last for several years, as cohorts of differing size and quality move through the population structure. In some coral reef fish, the signal of major temporal fluctuations in recruitment can span at least 10 years. Let us take a simple example to illustrate how a marked change of recruitment in a given year may generate delayed cohort effects on age structure, and thereby on demographic processes. Consider a vertebrate population in which all individuals give birth for the first time at age 4, produce two offspring per year between 4 and 8 years of age, then cease reproducing. Assume that the first-year survival is 0.75, the annual survival between 1 and 8 years of age is 0.90, and the annual survival beyond 8 years of age is 0.75. Running a simple pre-breeding Leslie matrix model (i.e., individuals observed just before a new cohort is produced so that all individuals are included from 1 year of age onward) leads to an asymptotic natural rate of increase of 1.15, with a stable age distribution of 56.15% individuals in the pre-reproductive stage, 36.14% in the prime-age stage, and 7.71% in the senior stage. Now let recruitment markedly decrease in a given year so that the first-year survival becomes 0.25 instead of 0.75. After the perturbation in recruitment, the natural rate of increase will decrease to 0.97 and the age structure 1 year later will be shifted toward old individuals with 48.01%, 42.86%, and 8.88% of animals in the pre-reproductive, prime-age, and senior stages, respectively. Four years after the perturbation a reverse trend in age structure would have occurred, with 60.68%, 31%, and 8.32% of animals in the pre-reproductive, prime-age, and senior stages, respectively, illustrating how the adult age structure in a population reflects the recruitment of juveniles some years before. The asymptotic growth rate will not be reached for 8 years after the perturbation. Thus, we can observe cycles in the rate of recruitment generated by the lagged reciprocal effects of recruitment variation on age structure and then of variation in age structure on recruitment. Such delayed numerical effects are pervasive in long-lived species.

Another delayed effect is generated by among-cohort differences in individual quality. Although less often addressed because of the requirement of long-term longitudinal data, such 'quality effects', often in propagule size, have marked effects on population dynamics. High-quality cohorts will thus not only produce more recruits than low-quality cohorts, but they may also produce recruits of higher quality that will reproduce earlier, and will give birth to more offspring of higher quality as compared to low-quality cohorts. These quality effects could potentially lead to multigenerational signatures of variability in recruitment, and deserve much greater attention.

See also: Age Structure and Population Dynamics; Demography; Dispersal–Migration.

Further Reading

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Remote Sensing

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Introduction	Summary
Remotely Sensed Data Sets for Ecological Modeling	Further Reading
Accuracy Assessment and Validation	

Introduction

Remotely sensed data and methods are used extensively to provide data layers for ecological modeling. Understanding fundamental remote-sensing concepts will help ecosystem modelers make informed decisions regarding the utility and limitations of the broad spectrum of remotely sensed data and their derived products.

The main focus of this article is to introduce remote-sensing science and associated data sets of potential relevance to ecological modeling. The article begins with an overview of fundamental remote-sensing concepts. This is followed by a section on how remotely sensed data can be used to derive a broad range of biophysical data sets that are useful for terrestrial and aquatic ecological modeling. Several of the more common data sets derived from remotely sensed data are described with comments about how the data sets are produced, their strengths, and limitations. The article concludes with a summary of accuracy and validation.

What Is Remote Sensing?

In general terms, remote sensing is the science and practice of acquiring information about an object without actually coming into contact with it. In terms more appropriate for our purposes remote sensing is a technology for sampling reflected and emitted electromagnetic (EM) radiation from the Earth's terrestrial and aquatic ecosystems and atmosphere. This is typically done by recording images from airplanes and satellites to help identify or better understand features on the Earth's surface. In this article we will discuss a wide set of techniques, often known by the alternative name of 'Earth observation' (EO). We will only address EM remote sensing, so geomagnetic and acoustic remote-sensing techniques (sonar and seismic sounding) will not be covered.

A simple example of a remote-sensing instrument is a photographic or digital camera. A camera records energy in the form of light that is reflected from a surface to form an image. Most photographic cameras record visible light so that when we look at the photograph the image resembles the feature that was photographed. More sophisticated remote-sensing instruments are able to record energy outside of the range of visible light. Data from remote-sensing instruments can be recorded as images or, in the case of lidar, a series of point data.

Brief History of Remote Sensing

For our purposes we will begin the history of remote sensing with the invention of the photographic camera in the early nineteenth century. In the 1840s photographs were taken from cameras secured to tethered balloons for purposes of topographic mapping. For the next 100 years or so camera technology improved but the major advances were in the platforms used to hold the camera systems. At first people experimented with platforms such as kites, rockets, and even pigeons. A major step forward was made with the invention of the airplane and the next leap occurred when cameras could be mounted